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EFFECTS OF RAPID FLIGHT-FEATHER MOLT ON POSTBREEDING DISPERSAL IN A PURSUIT-DIVING SEABIRD

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Abstract.—Breeding seabirds have been well studied but seabird ecology during the nonbreeding season is poorly understood because many species disperse far from breeding colonies to molt at sea. We characterized the timing of prebasic molt and postbreeding dispersal, described postbreeding dispersal movements, and estimated changes in body mass during molt for Marbled Murrelets (*Brachyramphus marmoratus*; Alcidae) in central California, 1999–2004. According to mark–recapture and at-sea surveys, 248–315 of 496–637 individuals (43–50%) used Año Nuevo Bay, located immediately adjacent to nesting areas, for their prebasic molt in August–October. Long-distance dispersal ($\geq$100 km) from Año Nuevo Bay by radiomarked Marbled Murrelets was low during breeding (9–13%, $n = 46$), but was greater for individuals radiomarked at the end of the breeding season (69–90%, $n = 20$). The mean dispersal dates were 18 May and 21 October for the breeding and postbreeding samples, respectively, and postbreeding dispersal occurred an average of two weeks after molt completion. Mean dispersal distances were 184 km and 256 km in the breeding and postbreeding periods, respectively. Of 12 long-distance dispersers, all moved south except one. Marbled Murrelets gained mass during molt ($n = 184$), except during a moderate El Niño event in 2002 when mass remained constant. However, birds did not take longer to molt in 2002, which suggests that individuals allocated more energy reserves to molt processes in that year. Apparently, sufficient prey resources were available in Año Nuevo Bay for both basic metabolic requirements and the demands of molt, even when water was moderately warm. *Received 11 July 2006, accepted 14 March 2007.*

Key words: body mass, *Brachyramphus marmoratus*, El Niño, energy demands, Marbled Murrelet, postbreeding dispersal, prebasic molt, seabird ecology.

Efectos de la Muda Rápida de las Plumas de Vuelo Sobre la Dispersión Post-Reproductiva en un Ave Marina que se Zambulle para Perseguir Presas

Resumen.—Las aves marinas han sido bien estudiadas durante los períodos de cría. Sin embargo, la ecología de estas aves durante los períodos no reproductivos es escasamente conocida debido a que muchas especies se dispersan grandes distancias desde sus colonias reproductivas para mudar sobre el océano. Caracterizamos los momentos en que ocurren la muda prebásica y la dispersión post-reproductiva, describimos los movimientos post-reproductivos y los cambios en el peso corporal durante la muda para *Brachyramphus marmoratus* (Alcidae) en California central entre 1999 y 2004. De acuerdo con muestreos hechos en el océano y de marcado-recaptura, 248–315 de 496–637 individuos (43–50%) utilizaron la bahía Año Nuevo, inmediatamente adyacente a las áreas de nidificación, para sus mudas prebásicas entre agosto y octubre. La dispersión a distancias grandes ($\geq$100 km) desde la bahía Año Nuevo por individuos de la especie *B. marmoratus* marcados con radiotransmisores fue baja durante la época de cría (9–13%, $n = 46$), pero fue mayor para individuos marcados con transmisores al final de la época reproductiva (69–90%, $n = 20$). La fecha de dispersión promedio fue el 18 mayo y el 21 de octubre para las muestras tomadas durante los períodos reproductivos y post-reproductivos, respectivamente. La dispersión post-reproductiva ocurrió, en promedio, dos semanas después de completar la muda. Las distancias promedio de dispersión fueron de 184 km y 256 km durante los períodos reproductivos y post-reproductivos, respectivamente. De 12 individuos que se dispersaron a distancias grandes, todos fueron hacia el sur excepto uno. Los individuos aumentaron de peso durante la muda ($n = 184$), excepto durante un evento moderado de El Niño en 2002, periodo durante el cual el peso permaneció constante. Sin embargo, las aves no demoraron más en mudar en 2002, lo que sugiere que en ese año los individuos asignaron más reservas energéticas a los procesos de muda. Aparentemente, existieron recursos presa suficientes en la bahía Año Nuevo, tanto para los requerimientos metabólicos básicos como para las demandas energéticas de la muda, incluso cuando el agua aumentó de temperatura.

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SEABIRDS HAVE BEEN well studied during the breeding season, but their ecology during the postbreeding period is poorly understood because many species disperse far from breeding colonies to molt at sea. The prebasic molt is a critical process in the annual cycle of seabirds, given that replacement flight-feathers maintain flight efficiency and new down facilitates thermoregulation in cold water. Molt requires considerable energy investment (Murphy 1996) and can double basal metabolic rates for extended periods (Ellis and Gabrielsen 2001). Many seabirds, including all members of the Alcidae except auklets, undergo a virtually simultaneous flight-feather molt following breeding that renders them flightless for several weeks (Bédard and Sealy 1984, Thompson et al. 1998, Thompson and Kitayski 2004). Thus, in addition to imposing significant energy demands, molt can severely limit foraging ranges and may negatively affect the foraging efficiency of pursuit-diving alcids for several weeks after breeding (Bridge 2004).

The constraints and energy demands associated with the prebasic molt provide an incentive for alcids to forage in waters with abundant and predictable prey resources during molt (Jehl 1990). Following fledging, many alcids disperse from at-sea areas used during the breeding season (Bradstreet 1982, Brown 1985, Piatt and Gould 1994, Gaston and Hipfner 2000), and the timing of dispersal in relation to molt includes (1) individuals undergoing a rapid prebasic molt immediately followed by long-distance dispersal (Bédard 1985), (2) molt occurring as individuals swim to wintering areas while caring for young (Ainley et al. 2002), and (3) molt occurring at wintering areas after postbreeding dispersal (Carter and Stein 1995). However, where and when molt occurs in relation to the timing of dispersal is unknown for many species, and few studies have described the at-sea movements of individuals after breeding (e.g., Adams et al. 2004).

Although molt imposes an energetic cost and constrains foraging, molting alcids no longer need to fly long distances to provision young (for species that have non-overlapping molting and breeding periods). Common Murres (*Uria aalge*) appear to regain breeding-season mass losses during molt (Ainley et al. 2002), and several other alcids achieve their greatest mass in the winter (Gaston 1994, Gaston and Jones 1998). However, the extent to which the demands of molt influence body mass likely depends on the availability of prey resources. Because studies of body condition during molt are rare, this relationship is not well understood.

We characterized the effects of rapid flight-feather molt on postbreeding dispersal in the Marbled Murrelet (*Brachyramphus marmoratus*; hereafter "murrelet"), a small alcid, listed as threatened in parts of the United States, that nests in old-growth forests along the west coast of North America. We studied the small, geographically isolated population that breeds in remnant old-growth Coast Redwood (*Sequoia sempervirens*) forests in the Santa Cruz Mountains of central California (Baker et al. 2006). This population occurs at sea primarily between Half Moon Bay and Santa Cruz during the breeding season (Becker et al. 1997, Becker and Beissinger 2003, Peery et al. 2006a). Murrelets in California typically fledge one young between mid-June and mid-September, and parents are not believed to care for young after fledging (Peery et al. 2007). Like most alcids, murrelets undergo a nearly simultaneous prebasic flight-feather molt that renders them flightless for several weeks following the breeding season (Carter and Stein 1995). In some populations, most individuals disperse before the prebasic molt (Carter and Stein 1995), and postbreeding murrelets may disperse hundreds of kilometers after breeding (Beauchamp et al. 1999).

We used radiotelemetry, mark–recapture methods, at-sea surveys, and molt information from murrelets captured at sea from 1999 to 2004 to (1) identify at-sea areas used for the prebasic molt, (2) characterize the nature of postbreeding dispersal movements, (3) characterize the timing of postbreeding dispersal in relation to the timing of the prebasic molt, and (4) assess the extent to which the demands and constraints of prebasic molt influenced body condition (proxied with body mass). Oceanographic conditions in the California Current System are strongly influenced by two- to seven-year recurrences of warm-water El Niño–Southern Oscillation (ENSO) conditions that increase sea-surface temperatures, reduce primary productivity, and ultimately affect the availability of food resources for upper-level predators like murrelets (Becker and Beissinger 2003, 2006; Becker et al. 2007). A moderate ENSO event occurred in fall 2002 (Venrick et al. 2003), which enabled us to evaluate the relationship between prebasic molt and body condition for murrelets in warmer versus cooler water.

METHODS

Characterizing dispersal with radiotelemetry.—We captured 46 murrelets early in the breeding season from 25 April to 16 May, 2000 and 2001 (breeding-season sample), and 20 murrelets on 13 and 14 September, 2002, after almost all fledging was expected to be complete (postbreeding-season sample). Murrelets were captured by night-lighting from a 4-m skiff (Whitworth et al. 1997) in Año Nuevo Bay, California (Fig. 1), as described by Peery et al. (2004a, b, 2006a, b). Murrelets were transported to a larger, 14-m vessel and radiomarked (Holohil BD-2G [2.2 g] and PD-2 [2.7 g] units with an estimated transmitting life of 12–20 weeks) using the subcutaneous-anchor method (Newman et al. 1999). Sex was determined using genetic techniques (Vanderkist et al. 1999). Año Nuevo Bay is located immediately adjacent to a major concentration of nesting habitat in the Santa Cruz Mountains and harbors high densities of murrelets during the breeding season (Becker and Beissinger 2003).

We tracked radiomarked murrelets using two- or four-element antennas mounted on trucks and fixed-wing aircraft. Telemetry surveys for murrelets captured in April and May, 2000–2001, were conducted every day between Half Moon Bay and Santa Cruz. When an individual was not located between Half Moon Bay and Santa Cruz, aerial surveys were conducted as far north as the Oregon–California border and as far south as the Los Angeles area, usually within four days of the individual going undetected. Birds captured in September 2002 were tracked using aerial surveys only, conducted one or two times per week from the Oregon–Washington border to Los Angeles. Aerial telemetry surveys in fall were conducted along the coastline on the outgoing leg and between 5 and 12 km offshore on the returning leg. Occasionally, only the nearshore transect was surveyed, or surveys were terminated prematurely because of weather or other constraints. Locations from ground surveys were obtained via triangulation, and locations obtained during aerial surveys were

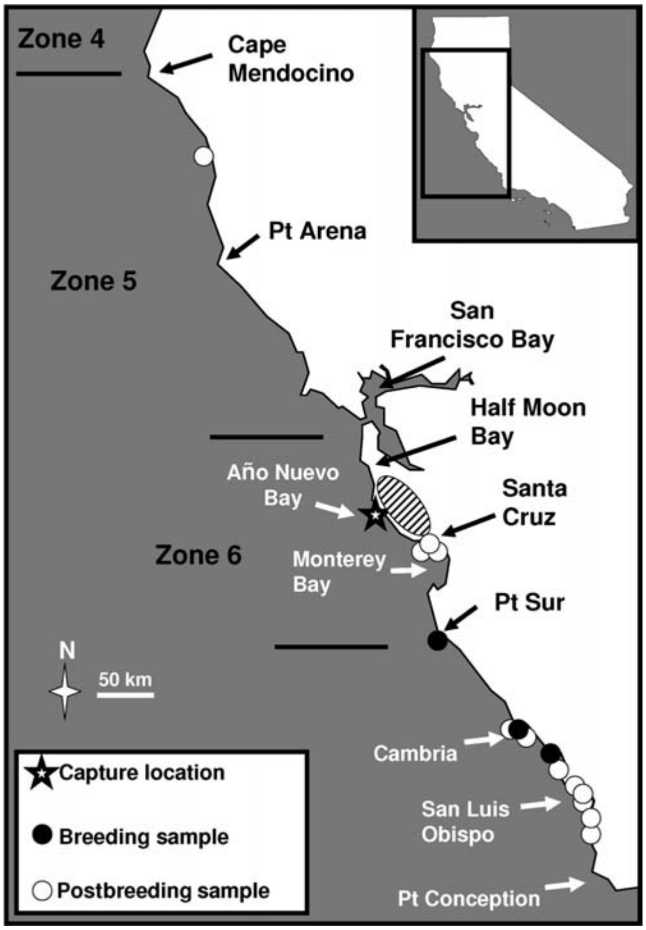

Fig. 1. Farthest dispersal locations for 15 Marbled Murrelets radiomarked in Año Nuevo Bay, California, early in the breeding season (24 April–16 May 2000–2001) and the postbreeding season (September 13–14 2002). All three dispersal movements by Marbled Murrelets in the breeding sample were >100 km to the south. Of the 12 Marbled Murrelets captured in the postbreeding season, 9 made long-distance dispersal movements (>100 km; 8 south and 1 north), and 3 made shorter movements (<31 km) to the south into northern Monterey Bay, California. Some symbols were slightly offset to reduce overlap. Hatched area indicates major concentration of Marbled Murrelet nesting habitat in the Santa Cruz Mountains. Zones refer to Conservation Zones delineated by the U.S. Fish and Wildlife Service (1997).

estimated using a geographic positioning system (GPS; estimated accuracy of locations <1.5 km). We defined dispersal distance as the greatest distance a radiomarked murrelet was located from its capture location in Año Nuevo Bay. We estimated dispersal date as the midpoint between the last date a murrelet was detected in Año Nuevo Bay and the first date it was detected at the location farthest from its capture location.

Estimating seasonal variation in at-sea abundance and distribution.—We estimated the abundance of murrelets of all age classes (juveniles and adults) in Año Nuevo Bay with mark–recapture methods during the prebasic molting period (August–October). We captured and banded 174 murrelets in Año Nuevo Bay during these months from 1999 to 2003 to estimate abundance from 2000 to 2003, as described by Peery et al. (2006a, b) (abundance could not be estimated in the first year of marking). Except for radiomarked murrelets, all individuals were banded and processed (see below) aboard the 4-m skiff. We did not recapture enough individuals within years to use closed-population models and instead used Cormack-Jolly-Seber (CJS) mark–recapture models for open population designed to estimate annual survival (φ_t; the probability of surviving from year t to $t+1$) and recapture (p_t; the probability of a banded individual being captured in year t given that it was alive) probabilities (Cormack 1964, Jolly 1965, Seber 1965). Four competing CJS models were constructed in MARK (White and Burnham 1999) in which survival and recapture probabilities varied among years or were constant among years. Support for competing models was evaluated usingAkaike's Information Criterion (AICc) model weights (Burnham and Anderson 2002). Survival probabilities were treated as nuisance parameters required for the estimation of recapture probabilities, which were used to estimate the number of individuals (N) in Año Nuevo Bay in year t as

$$\widehat{N}_t = \frac{(n_t + 1)\widehat{M}_t}{m_t + 1}$$

where $\widehat{M}_t = m_t/\widehat{p}_t$, n_t was the total number of individuals captured in year t, and m_t was the number of previously banded individuals captured in year t, following Franklin et al. (1996).

We estimated seasonal changes in density of murrelets using at-sea surveys from 1999 to 2004 in four areas that were believed, on the basis of previous work (Carter and Erickson 1992, Becker et al. 1997) and our knowledge of the area, to contain high densities. These locations were Año Nuevo Bay (4 km of coastline), Half Moon Bay to Santa Cruz (~75 km, which included Año Nuevo Bay), Monterey Bay (24 km), and just north of Cambria, in San Luis Obispo County (18 km) (Fig. 1). All surveys except those between Half Moon Bay and Santa Cruz were conducted along line transects parallel to the coastline, 400–500 m from shore. Surveys between Half Moon Bay and Santa Cruz were conducted along zigzag transects 200–1,350 m from shore.

Two observers recorded all murrelet sightings, including group size and estimated distance from the transect line. The detection data were analyzed using DISTANCE software to estimate survey-specific densities (Buckland et al. 2001). Surveys were conducted in different boats and by different observers in different phases of the study. For this reason, separate detection functions were generated for five different subsets of data: surveys conducted in Año Nuevo Bay in June, July, and August 1999–2000 ($n = 15$), from October 1999 to April 2000 ($n = 21$), from October 2001 to May 2002 ($n = 21$), from Half Moon Bay to Santa Cruz from June 2002 to September 2002 ($n = 17$), and year-round in Monterey Bay from 1999 to 2001 ($n = 34$). Because relatively few murrelets were detected during surveys in San Luis Obispo County (July–November 2004; $n = 4$), all these individuals were pooled with data from Año Nuevo Bay collected from October 1999 to April 2000 (observer height was similar between these surveys, ~2 m above the water). We used AIC to select the best detection model for each data subset, and survey-specific densities ($\widehat{D}$; birdsper square kilometer) were estimated as

$$\widehat{D} = \frac{\widehat{E}(n)\widehat{f}(0)\widehat{E}(s)}{2L}$$

where $\widehat{f}(0)$ is the value of the probability density function of perpendicular distances from the transect line evaluated at zero distance, $\widehat{E}(n)$ is the expected number of groups, $\widehat{E}(s)$ is the expected number of birds per group, and L is the length (km) of the line transect (Buckland et al. 2001). Survey-specific density estimates were averaged to obtain monthly density estimates for each area

Dynamics of molt and seasonal changes in body mass.— We scored primary molt and sexed 187 after-hatch-year (AHY) murrelets ($\geq$1 year old; see Peery et al. [2006b] and Beissinger and Peery [2007] for a description of aging criteria) captured in Año Nuevo Bay from August to October, 2000–2003 (murrelets captured in 1999 were not scored). For each bird, all 10 primary feathers on both wings were inspected and assigned a molt score from 0 to 10 (0 = old feather still present, 1 = feather missing to new feather 20% grown, 3 = 21–40% grown, 5 = 41–60% grown, 7 = 61–80% grown, 9 = 81–99% grown, and 10 = 100% grown). Molt scores were summed for each wing. The mean of the scores for the two wings was calculated for a total primary molt score ranging from 0 to 100, which approximated the percentage of primary molt that had been completed at the time of capture.

We estimated the mean molt duration for individuals and the expected duration for the entire population based on the strength of the relationship between Julian date and primary molt score. Regressing date against molt score and molt score against date provides estimates of individual and population-level molt duration, respectively (Pimm 1976, Thompson et al. 1998). However, instead of simple regression models, we used analysis of covariance (ANCOVA) models that allowed for the inclusion of sex and ENSO (ENSO vs. non-ENSO years) categorical effects and associated interaction terms so that we could compare the duration and timing of molt between ENSO and non-ENSO years and between males and females. Testing the significance of sex and ENSO effects yielded a comparison of the timing of molt initiation between males and females and between ENSO and non-ENSO years, respectively. Testing the significance of the interaction between sex and molt score and between ENSO status and molt score yielded a comparison of molt duration between males and females and between ENSO and non-ENSO years, respectively.

We captured and weighed 338 murrelets from April to October, 1999–2003, with a 500-g Pesola scale. Monthly differences in body mass were compared between the 2002 ENSO year and all other years pooled using a three-factor ANOVA model with ENSO, month, and sex as categorical effects. Because of small sample sizes, data from April and May were pooled, and data from June and July were pooled.

We also estimated changes in body mass of murrelets during prebasic molt on the basis of 184 AHY murrelets captured, weighed, scored for primary molt, and sexed in August–October, 2000–2003. A decrease in body mass should occur if murrelets were not able to meet the energetic costs of molt, whereas body mass should increase if murrelets foraged at an energetic surplus. We compared the rate of mass change during the 2002 ENSO event to the rate of mass change during the three non-ENSO years using an ANCOVA model, where molt score was the dependent variable, mass was a continuous independent variable, and ENSO and sex were categorical effects. Means are presented with standard error (SE) unless otherwise noted.

RESULTS

Timing and nature of dispersal movements.—Three of 46 murrelets (7%) radiomarked in our breeding-season sample dispersed considerable distances (i.e., $\geq$100 km) from Año Nuevo Bay during the breeding season (Table 1 and Fig. 1). However, mean radiolife (~60 days) was considerably lower than expected, and some murrelets could have dispersed after transmitters failed without being detected. Excluding individuals that were tracked <30 and

TABLE 1. Primary molt status and distance, location, and timing of the dispersal for 12 Marbled Murrelets radiomarked in Año Nuevo Bay, California in April and May of 2000-2001 and September of 2002. Positive (negative) distances indicate dispersal to the north (south).

Bird ID	Sex	Days tracked	Molt score	Estimated molt completion	Dispersal date	Dispersal distance (km)	Dispersal location
April-May 2000-2001							
162	F	88	—	—	4 May	−138	San Luis Obispo area
463	F	108	—	—	6 June	−193	San Luis Obispo area
939	M	74	—	—	13 May, 9 June[a]	−220	San Luis Obispo area
September 2002							
043	M	48	44	3 Oct	5 Oct	−192	San Luis Obispo area
102	M	39	48	2 Oct	13 Oct	−193	San Luis Obispo area
182	F	85	10	15 Oct	8 Nov, 2 Dec[a]	+318	Point Arena
218	M	95	5	16 Oct	18 Nov	−288	San Luis Obispo area
241	M	81	9	15 Oct	30 Oct	−262	San Luis Obispo area
419	F	115	10	15 Oct	6 Oct, 24 Nov[a]	−287	San Luis Obispo area
451	F	106	100	6 Oct	6 Oct	−261	San Luis Obispo area
489	F	39	46	2 Oct	19 Oct	−234	San Luis Obispo area
641	M	53	9	8 Oct	13 Oct	−273	San Luis Obispo area

[a] These birds dispersed, returned to the vicinity of the capture area, and dispersed again; both dispersal dates are given.

<60 days, 3 of 35 murrelets (9%) and 3 of 24 murrelets (13%) dispersed considerable distances, respectively. Tracking was terminated by 13 August 2000 and by 1 August 2001 because of the small number of transmitters emitting signals. All dispersal was to the south, and the mean (± SD) dispersal distance was 184 ± 42 km (range: 138–220 km). Dispersal generally occurred early in the breeding season; the mean date of "first" dispersal (see below) was 18 May (±17 days [SD]; range: 4 May–6 June). None of the three dispersers was ever detected inland visiting nesting habitat in the Santa Cruz Mountains, but murrelet 162 had a partially formed brood patch when captured (Peery et al. 2004a, b).

Nine of the 20 murrelets (45%) radiomarked in our postbreeding sample dispersed >100 km from Año Nuevo Bay (Table 1 and Fig. 1). As with the breeding-season sample, mean radio-life (~47 days) was considerably less than expected. Excluding individuals that were tracked <30 and <60 days, 9 of 13 murrelets (69%) and 9 of 10 murrelets (90%) dispersed considerable distances, respectively. Eight of these murrelets dispersed south an average of 249 km, and one bird moved 318 km to the north (overall mean dispersal distance: 256 ± 43 [SD] km; range: 192–318 km). An additional three murrelets shifted their distribution south much shorter distances (<31 km) into northern Monterey Bay, where murrelet densities were high in fall and winter according to at-sea surveys (Fig. 2; see below). None of the remaining murrelets was detected outside of Año Nuevo Bay, but these individuals were generally tracked for <30 days. The nine long-distance dispersers first vacated Año Nuevo Bay between 5 October and 18 November (mean dispersal date: 21 October, ± 15 [SD] days). These individuals were detected only on the nearshore transect (along the coastline) and never on the offshore transect (≥5 km from shore).

Radiomarked murrelets remained within relatively small areas after dispersing from Año Nuevo Bay. Twelve percent of all movements exceeded 160 km, but >83% of all movements were <40 km. In general, larger movements reflected dispersal events from Año Nuevo Bay to early wintering areas, whereas shorter distances reflected local foraging movements around Año Nuevo Bay before dispersal and at early wintering areas following dispersal. However, one long-distance disperser in the breeding sample and two long-distance dispersers in the postbreeding sample dispersed several hundred kilometers, then returned to the Año Nuevo Bay area and, within 24–48 days, again moved to the general area they used after their first dispersal movement (Table 1).

Seasonal variation in abundance and distribution.—The best mark–recapture model contained time-constant recapture ($\widehat{p} = 0.134 \pm 0.040$) and survival probabilities ($\widehat{\phi} = 0.857 \pm 0.117$) from 2000 to 2003. According to AIC_C weights, this model was >14× more likely than any of the other three competing models, and the estimate of recapture probability from this model was used to estimate abundances for all four years. We estimated that 248 to 315 murrelets (mean = 283) were present in Año Nuevo Bay from August to October in 2000–2003 (Table 2). On the basis of at-sea surveys, Peery et al. (2006a) estimated that the mean size of the murrelet population in central California was 594 individuals (range: 496–637) during the same four years. Thus, an average of 48% (range: 43–50%) of the total central California murrelet population used Año Nuevo Bay during the prebasic molting period (Table 2).

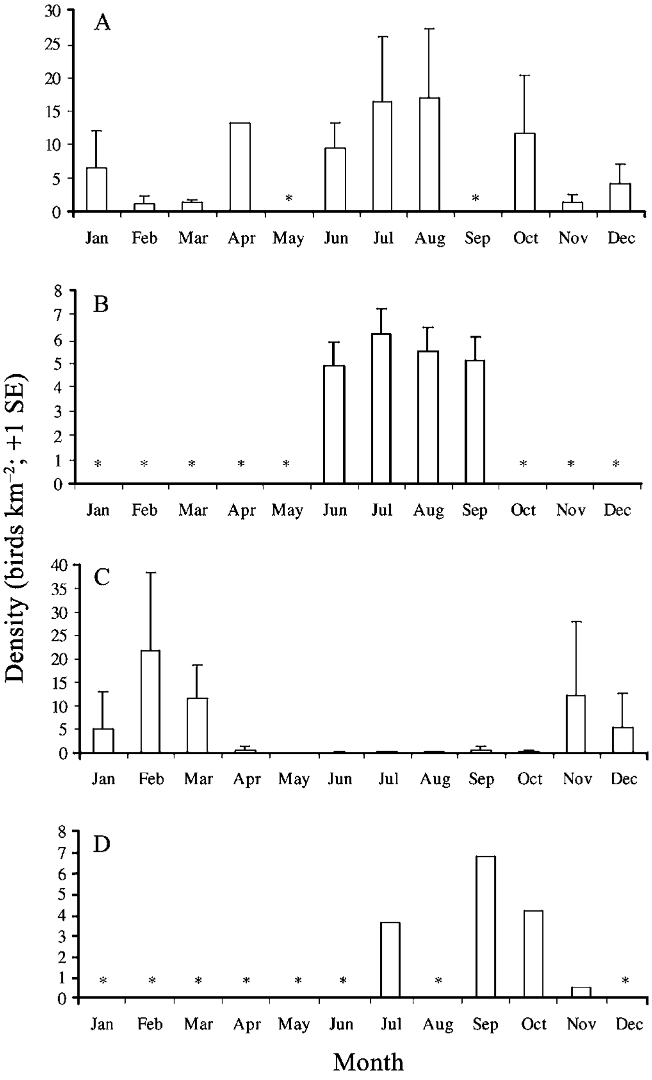

Fig. 2. Mean monthly density estimates for Marbled Murrelets in (A) Año Nuevo Bay, (B) Half Moon Bay to Santa Cruz, (C) Monterey Bay, and (D) San Luis Obispo County, California, based on at-sea surveys and line-transect methods. Asterisks indicate that surveys were not conducted in a given month (e.g., surveys not conducted in Año Nuevo Bay in September).

According to at-sea surveys, densities of murrelets in Año Nuevo Bay were greatest from April through October (Fig. 2A). Surveys were not conducted in September, but mark–recapture results indicated that density was also high during that month. Consistent with the dispersal behavior of radiomarked murrelets, densities declined considerably in Año Nuevo Bay from October to November. Densities were high from Half Moon Bay to Santa Cruz from June through September, indicating that most postbreeding dispersal away from breeding areas in the Santa Cruz Mountains did not occur until after September. Densities in Monterey Bay began increasing in November, after the decline in Año Nuevo Bay, and exceeded 20 murrelets per square kilometer in February

Table 2. Mark–recapture estimates of the abundance of Marbled Murrelets of all age classes using Año Nuevo Bay (ANB; 95% CL), California, during the prebasic molting period ($n = 174$ banded Marbled Murrelets, August–October) and estimates of total population size in central California (95% CL) from at-sea surveys conducted by Peery et al. (2006a) in the breeding season. "Proportion in ANB" is an estimate of the proportion of the total central California Marbled Murrelet population that used ANB during the prebasic molting period.

Year	ANB abundance	Total abundance	Proportion in ANB
2000	248 (159–507)	496 (338–728)	0.50
2001	274 (177–562)	637 (441–920)	0.43
2002	315 (194–616)	628 (487–809)	0.50
2003	296 (181–575)	615 (463–815)	0.48
All years	**283 (264–302)**	**594 (529–659)**	**0.48**

(Fig. 2C). Off the coast of San Luis Obispo County, murrelets were detected from July through November, with the greatest density occurring in September (Fig. 2D).

Timing and duration of molt.—Of the 187 AHY murrelets captured and molt-scored in August–October, 2000–2003, 167 (89%) were molting their primaries (molt score >0 and <100), 5 (3%) had not started molting, and 15 (8%) had completed their molt. Nineteen of the 20 radiomarked murrelets (95%) were molting their primaries when captured, and the remaining individual had completed its primary molt.

We excluded individuals not actively molting when estimating mean individual molt duration with the ANCOVA model (thus, $n = 167$). According to this model, primary molt score was a significant predictor of Julian date ($F = 65.13$, df = 1 and 161, $P < 0.01$) and explained 31% of the variation in Julian date (Fig. 3A). Excluding other model effects (sex and ENSO status), this relationship can be expressed as Julian date = 0.370 × molt score + 237.3, which indicates that individual murrelets took an average of 37 ± 4 days to complete their primary molt. Mean primary-molt initiation date was 25 August, and mean molt completion was 3 October (±2 days). Murrelets did not take longer to molt their primaries during the 2002 ENSO event than in non-ENSO years, as indicated by the lack of a significant interaction between primary molt score and the ENSO effect ($F = 0.18$, df = 1 and 161, $P = 0.68$). Nor was there a difference in molt duration between males and females, as indicated by the lack of a significant interaction between molt score and sex ($F = 1.25$, df = 1 and 161, $P = 0.27$). There was no significant difference in the timing of molt initiation between ENSO and non-ENSO years ($F = 3.45$, df = 1 and 161, $P = 0.07$) or between males and females ($F = 1.00$, df = 1 and 161, $P = 0.32$). Moreover, the timing of molt was highly synchronous between males and females that were captured together ($r = 0.95$, $P < 0.01$, $n = 21$ pairs; Fig. 4).

According to the ANCOVA model used to estimate population-level molt duration, Julian date was a significant predictor of primary molt score ($F = 64.90$, df = 1 and 161, $P < 0.01$) and explained 31% of the variation in primary molt score (Fig. 3B). Excluding other model effects (sex and ENSO status), this relationship can be expressed as molt score = 0.838 × Julian date − 179.1, which indicates that population-level molt

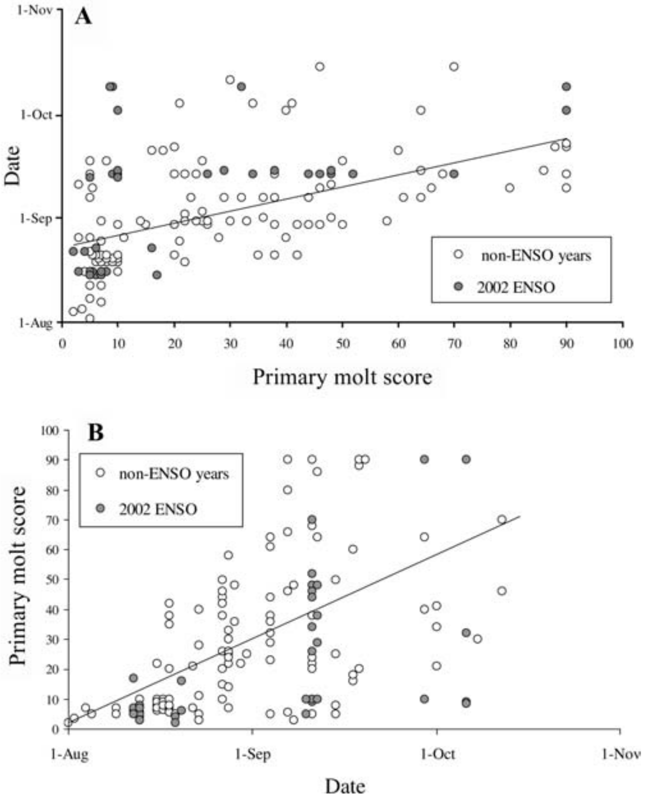

Fig. 3. Progression of primary molt for 167 Marbled Murrelets molting in Año Nuevo Bay, California, August–October, 2000–2003. (A) Date regressed against primary molt score to estimate individual molt duration. (B) Primary molt score regressed against date to estimate population-level molt duration. Both regression lines were based on data pooled for the 2002 ENSO year and non-ENSO years because no difference in slope or intercept was detected. Twenty individuals with primary molt scores of 0 or 100 were not included.

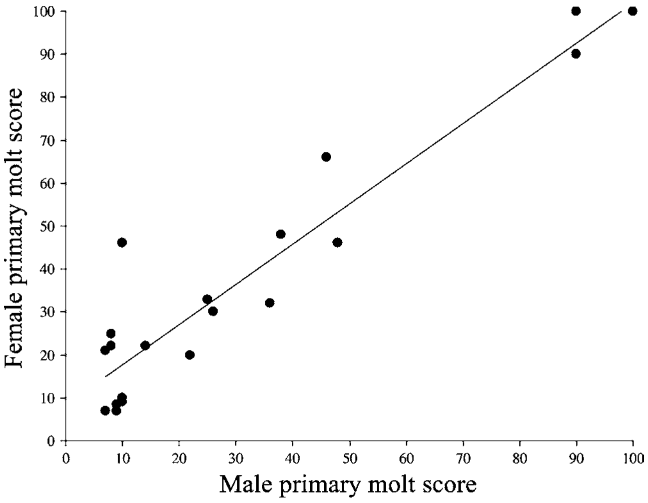

Fig. 4. Synchrony in the primary molt of 21 paired male and female Marbled Murrelets captured in Año Nuevo Bay, California, August–October, 2000–2003.

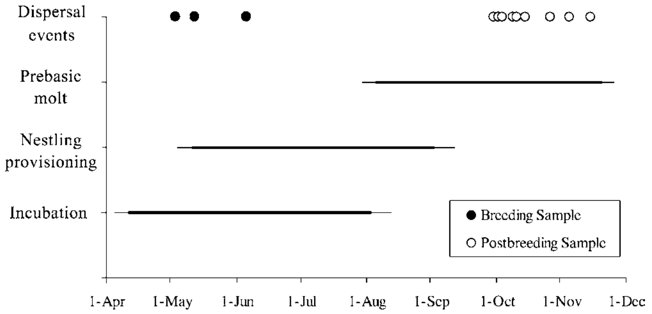

FIG. 5. Timing of postbreeding dispersal for 12 Marbled Murrelets in relation to population-level timing of breeding and prebasic molt in central California. Thicker lines indicate when 90% of breeding or molt occurred, and thinner lines encompass the entire breeding or molting period. Some symbols for dispersal events were slightly offset to reduce overlap. The timing of incubation and nestling provisioning were estimated using data and methodology presented in Peery et al. (2007).

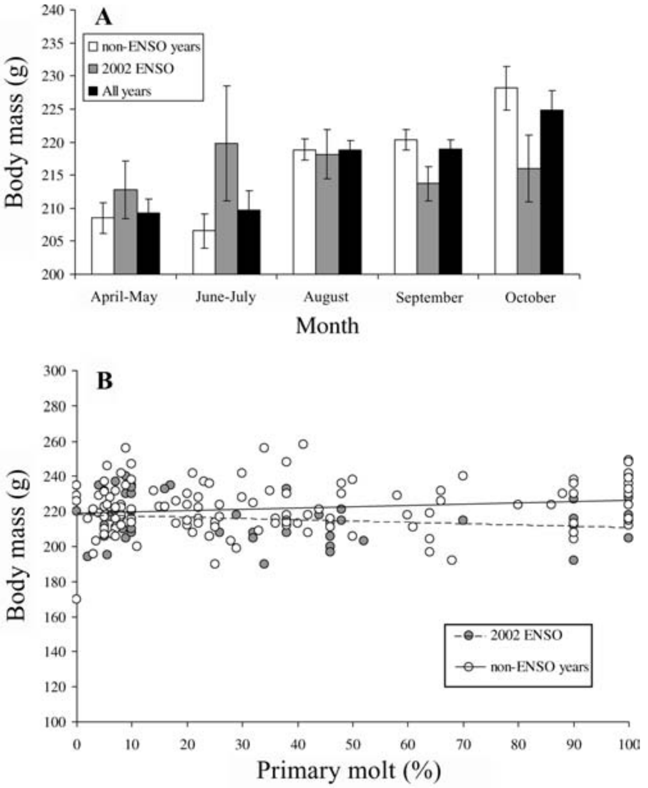

FIG. 6. Body mass (g; ± SE) of (A) 338 Marbled Murrelets captured from April through October, 1999–2003, in Año Nuevo Bay, California; and (B) 184 Marbled Murrelets captured and scored for molt in Año Nuevo Bay, California, from August through October, 2000–2003.

duration was 120 ± 11 days, started on 2 August, and ended on 29 November (±34 days). No difference in the duration or timing of population-level molt was detected between the 2002 ENSO year and non-ENSO years or between sexes (all $P > 0.05$).

Dispersal by murrelets radiomarked in the postbreeding sample occurred in the second half of the prebasic molting period, well after breeding was complete (Fig. 5). For the nine murrelets that moved long distances, dispersal occurred an average of 14 days after estimated completion of the individual's molt (range: −8 to 33; Table 1). Later-molting murrelets tended to disperse after early-molting murrelets, as evidenced by the nearly significant negative relationship between dispersal date and molt score ($F = 3.87$, df = 1 and 7, $P = 0.09$, $R^2 = 0.35$).

Seasonal changes in body mass.—When all murrelets captured from April to October ($n = 338$) were considered, body mass did not differ significantly between the 2002 ENSO year and non-ENSO years ($F = 0.04$, df = 1 and 320, $P = 0.83$) or between sexes ($F = 1.06$, df = 1 and 320, $P = 0.30$), but did differ significantly among months ($F = 3.06$, df = 5 and 320, $P < 0.02$). Body mass was relatively low from April to July and increased from August to October (Fig. 6A). According to t-tests of least-square means, body mass in April–May was significantly lower than in all other months (all $P < 0.05$) except June and July. Body mass in October was significantly greater than in June and July ($P = 0.04$), but no other comparisons were significant (all $P > 0.05$). A significant interaction existed between ENSO and month ($F = 2.71$, df = 5 and 320, $P = 0.03$), which indicates that differences in body mass among months were not consistent between ENSO and non-ENSO years, largely because murrelet body mass did not increase from April to October in 2002 (Fig. 5A).

When only murrelets captured in August–October were considered, body mass did not change significantly as individuals progressed in their primary molt ($F = 0.20$, df = 1 and 178, $P = 0.65$, $n = 184$) and did not differ between ENSO and non-ENSO years ($F = 0.12$, df = 1 and 178, $P = 0.73$) or sexes ($F = 1.39$, df = 1 and 178, $P = 0.24$). However, the rate of mass change differed significantly between non-ENSO years and the 2002 ENSO year (molt score by ENSO interaction: $F = 3.98$, df = 1 and 178, $P = 0.05$; Fig. 6B). Murrelets gained mass at a rate of 0.09 ± 0.037 g per 1% of molt completed (9.0 g total) during non-ENSO conditions ($t = 2.45$, df = 1 and 178, $P = 0.02$), but the slope of body mass regressed against molt score (−0.057 ± 0.064 g per 1% of molt completed) did not differ significantly from zero during the ENSO year ($t = 0.88$, df = 1 and 178, $P < 0.38$) (Fig 6B). The rate of mass change with respect to molt score did not differ between males and females ($F = 1.39$, df = 1 and 178, $P = 0.24$).

DISCUSSION

Postbreeding dispersal and its relationship to molt.—Our study indicates that most murrelets in central California undergo their prebasic molt immediately adjacent to nesting areas and then disperse tens to hundreds of kilometers south following the completion of molt. A low level of dispersal by murrelets radiomarked in Año Nuevo Bay occurred during the breeding season (9–13%), but dispersal was much higher starting in October (69–90%). All murrelets radiomarked in our postbreeding sample had already initiated molting before capture, and this sample could have been biased toward individuals that remained in Año Nuevo Bay for their prebasic molt. However, murrelet abundance and density remained high in Año Nuevo Bay through October (Table 2 and Fig. 2A; see also Strachan et al. 1995), indicating that little dispersal occurred before molt. About half the central California population used Año Nuevo Bay for the prebasic molt, according to mark–recapture analysis, but we strongly suspect that a significantly greater proportion of the population remained and molted between Half Moon Bay and Santa Cruz, given that densities in these waters did not decline from June through September (Fig. 2D).

Murrelets probably used Año Nuevo Bay for their prebasic molt because it is near a highly productive upwelling center and is sheltered from prevailing northwesterly winds and swell (Becker and Beissinger 2003, M. Z. Peery pers. obs.). Northern Anchovy (*Engraulis mordax*) and Night Smelt (*Spirinchus starski*), which are likely murrelet prey species in central California (Burkett 1995, Becker and Beissinger 2006, Becker et al. 2007), are abundant in these waters during fall (Henkel and Harvey 2006). Murrelets nest in relatively low densities and may have more incentive to molt in waters immediately adjacent to breeding areas than colonial seabirds that are more likely to deplete local prey resources around breeding sites (Ashmole 1963, Furness and Birkhead 1984, Birt et al. 1987). A possible explanation for the dispersal of radiomarked murrelets after molt is a change in the relative abundance and predictability of suitable prey between Año Nuevo Bay and early-wintering areas, because the abundance of small prey fish in Año Nuevo Bay can decline rapidly in late fall–early winter (Henkel and Harvey 2006).

Postbreeding dispersal is apparently a general phenomenon in this species, given that murrelets in Barkley Sound, British Columbia, also move away from waters adjacent to nesting habitat after the breeding season (Carter and Stein 1995) and murrelets radiomarked in southeastern Alaska dispersed up to several hundred kilometers from nesting areas (S. H. Newman unpubl. data). However, murrelets in central California generally dispersed after molting, whereas most of the Barkley Sound population dispersed from waters adjacent to nesting areas to molt in other locations, even though the timing of molt was similar between the two populations (central California: early August through November; Barkley Sound: mid-July to mid-November; Carter and Stein 1995). Assuming that the timing of dispersal is adaptive, the potential benefit of moving to another location, where food is more abundant or predictable, appears to outweigh costs associated with early dispersal in Barkley Sound, but not in California. Population-level differences in the timing of dispersal in relation to prebasic molt also have been observed in Dovekies (*Alle alle*) (Bradstreet 1982, Bédard 1985).

Although most murrelets dispersed after the prebasic molting period in the present study, individuals exhibited variation in the timing of postbreeding dispersal in relation to molt, and at least some birds molted at a significant distance from breeding sites. Breeding constraints certainly influence the timing of dispersal, given that two of the three radiomarked murrelets that dispersed south during the breeding season were nonbreeders (as indicated by the lack of a brood patch); the third had a partially formed brood patch but was never detected inland visiting nesting habitat and could have been an early failed breeder (Peery et al. 2004a, b). Six of 18 murrelets (33%) observed in the San Luis Obispo area during at-sea surveys conducted from August to October exhibited signs of molt; these birds could also have been early dispersers from nesting areas in the Santa Cruz Mountains, but they may have been subadults or nonbreeders that resided in the San Luis Obispo area year-round (breeding is not believed to occur south of Monterey Bay; Carter and Erickson 1992).

Murrelets visit inland nesting areas in the Santa Cruz Mountains at a reduced level throughout the nonbreeding season, except during the prebasic molt (Naslund 1993). We suspect that visitation of nest sites in winter is largely by the segment of the central California murrelet population that winters in northern Monterey Bay (about 30–50 km south of nesting habitat) and that birds wintering in the San Luis Obispo area (about 200–300 km south of nesting habitat) visit nesting areas much less frequently.

Constraints and costs of molt.—The fact that mean population-level molt duration (120 days) was much greater than the mean duration of individuals (37 days) indicates that the timing of molt was highly asynchronous among individuals. Asynchrony in the timing of molt in murrelets is very likely attributable to the high level of asynchrony in the timing of breeding (Peery et al. 2007), because a flightless molt is incompatible with breeding that occurs inland. In turn, asynchronous molt probably results in variation among individuals in the timing of postbreeding dispersal, given that dispersal often occurred within a couple of weeks of molt completion and early-molting murrelets tended to disperse after later-molting murrelets.

The lower body mass of murrelets during the breeding season than afterward is typical of alcids and is generally considered to be an adaptation that reduces the energetic costs associated with provisioning young (Croll et al. 1991, Gaston and Jones 1989; but see Hull et al. 2002). Under "normal" oceanographic conditions, murrelets in this study gained mass after the breeding season, when they no longer attended nest sites. Apparently, murrelets foraged at an energetic surplus and recovered from breeding-season mass loss despite the energetic costs of molt. By contrast, murrelets did not increase in body mass in the fall during the 2002 ENSO event and weighed an average of 12.2 g less in October 2002 than in October of other years. However, even during the ENSO event, molting murrelets did not lose a statistically significant amount of mass, which suggests that enough prey was available in Año Nuevo Bay to meet the energetic demands of molt and basic metabolic needs. There are other possible explanations for the absence of an increase in body mass in fall 2002, but ENSO effects on prey availability seem the most likely, given the tight coupling of murrelet diet and reproductive success with the large-scale oceanographic processes that influence sea-surface temperatures (Becker and Beissinger 2006, Becker et al. 2007).

Assuming that prey availability was reduced during the 2002 ENSO and that molt incurs a significant energetic cost, murrelets might be expected to have taken longer to molt their primaries in 2002 than in other years (Harris and Wanless 1990), but they did not. Compared to other years, murrelets may have allocated more energy to molt than to other metabolic needs during the 2002 ENSO to maintain a "normal" molt rate. Rapid molt reduces the time foraging is restricted to a small area and murrelets are especially susceptible to predators. Gaining mass provides a buffer against future, potentially adverse, foraging conditions but may not be as critical to the immediate survival of murrelets as the rapid growth of new flight feathers. By comparison, the demands of extended breeding can slow molt in auklets of the genera

Ptychoramphus and *Aethia* (Bédard and Sealy 1984, Emslie et al. 1990), but gradually molting auklets retain flight ability and have more flexibility to increase the duration of molt.

Conservation implications.—Oil spills, human disturbance, and depletion of fisheries could affect murrelet populations during the prebasic molt, because murrelets cannot readily escape the effects of such phenomena by flying to alternative foraging areas. Año Nuevo Bay is clearly an important postbreeding area, because mark–recapture analyses indicated that approximately half of the central California breeding population uses these waters for prebasic molt (Table 2). Moreover, considerably more than half the population likely molts immediately adjacent to nesting habitat in the Santa Cruz Mountains (between Santa Cruz and Half Moon Bay), given that mark–recapture work was restricted to Año Nuevo Bay and murrelets are found in relatively high densities throughout these waters until at least September (Fig. 2B).

Our results also indicate that northern Monterey Bay and the San Luis Obispo area (particularly the waters between Point Sur and Point Sal) are important wintering areas in central California. The 11 radiomarked murrelets dispersing south to the San Luis Obispo area traveled well beyond the southern boundary of Conservation Zone 6 at Point Sur (U.S. Fish and Wildlife Service 1997). Moving this boundary south to Point Conception could afford murrelets greater protection from anthropogenic disturbances during winter. However, postbreeding movement patterns and winter distributions may vary from year to year, and our postbreeding radiotelemetry work was conducted only in the 2002 ENSO year. In typical years, such heavy use of the San Luis Obispo area may not occur and more murrelets may occur in northern Monterey Bay, where densities can be very high in winter (Fig. 2C).

The northward dispersal by murrelet 182 to within ~75 km of Cape Mendocino (Table 1, and Fig.1) suggests that some mixing of murrelet populations could occur and that localized anthropogenic factors could affect multiple populations. Another radiomarked murrelet from the central California breeding population moved to waters near Cape Mendocino in the breeding season (E. E. Burkett unpubl. data), which indicates that the aforementioned dispersal event was not an isolated occurrence. Southerly dispersal by murrelets from northern California breeding populations of similar magnitude to dispersal distances estimated in the present study (200–300 km) could result in the mixing of populations in central California as well.

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