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INDIVIDUAL AND TEMPORAL VARIATION IN INLAND FLIGHT BEHAVIOR OF MARBLED MURRELETS: IMPLICATIONS FOR POPULATION MONITORING

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Abstract. We studied the inland flight behavior of 46 radio-marked Marbled Murrelets (*Brachyramphus marmoratus*) in 2000 and 2001 in central California to determine how the frequency of inland flights varied among individuals and over time. All breeding murrelets regularly flew inland (mean 82% of daily surveys), but we observed considerable variation in the inland flight behavior of non-nesters. Non-nesters that were physiologically in breeding condition (potential breeders) regularly flew inland (90% of individuals; mean 41% of daily surveys), but non-nesters that were not in breeding condition (nonbreeders) rarely flew inland (20% of individuals; mean 1% of daily surveys). The mean percentage of surveys on which individual murrelets flew inland increased from 20% in 2000 to 61% in 2001, which was partly due to an increase in the percentage of breeders from 11% in 2000 to 50% in 2001. The frequency of inland flights was greatest during the incubation and chick-provisioning stages (100% in both stages), and lowest during the pre- and postbreeding stages (70% and 78%, respectively). Although the mean percentage of flights increased dramatically between years, the regional population estimate from at-sea surveys increased only 28% from 496 to 637 individuals during the same period, indicating that monitoring techniques such as radar that count inland flights are more likely to reflect annual variation in breeding effort than changes in regional population size. Moreover, the inland flight behavior of potential breeders indicates that radar surveys will overestimate breeding population size, even though the lack of inland flights by nonbreeders indicates that radar surveys will underestimate regional population size.

Key words: Brachyramphus marmoratus*, breeding, inland flights, Marbled Murrelet, population monitoring, radar, radio-telemetry.*

Variación Individual y Temporal en el Comportamiento de Vuelo Tierra Adentro de *Brachyramphus marmoratus*: Implicancias para el Monitoreo de Poblaciones

Resumen. Estudiamos el comportamiento de vuelo tierra adentro de 46 individuos de *Brachyramphus marmoratus* marcados con radio transmisores durante el 2000 y 2001 en California central para determinar cómo la frecuencia de vuelos tierra adentro varió entre individuos y a lo largo del tiempo. Todos los individuos reproductivos de *B. marmoratus* volaron regularmente tierra adentro (media 82% de los muestreos diarios), pero observamos considerable variación en el comportamiento de vuelo tierra adentro en los individuos que no nidificaban. Los individuos que no nidificaban pero que se encontraban fisiológicamente en condición reproductiva (reproductores potenciales) volaron regularmente tierra adentro (90% de los individuos; media 41% de los muestreos diarios), pero los individuos que no nidificaban y que no se encontraban en condición reproductiva raramente volaron tierra adentro (20% de los individuos; media 1% de los muestreos diarios). El porcentaje medio de los muestreos en los cuales los individuos de *B. marmoratus* volaron tierra adentro incrementó de un 20% en el 2000 a un 61% en el 2001, lo que se debió parcialmente a un

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incremento en el porcentaje de individuos reproductivos de un 11% en el 2000 a un 50% en el 2001. La frecuencia de vuelos tierra adentro fue mayor durante las etapas de incubación y suministro de alimento a los pichones (100% en ambas etapas), y fue menor durante las etapas pre- y post-reproductivas (70% y 78%, respectivamente). Aunque la proporción media de vuelos incrementó dramáticamente entre años, la población regional estimada a partir de muestreos en el mar incrementó sólo 28% de 496 a 637 individuos durante el mismo período, indicando que las técnicas de monitoreo como el radar, que cuentan los vuelos tierra adentro, tienen una mayor probabilidad de reflejar la variación anual en el esfuerzo reproductivo que en los cambios de tamaño poblacional regional. Más aún, el comportamiento de vuelo tierra adentro de los reproductores potenciales indica que los muestreos con radar sobrestimarán el tamaño poblacional reproductivo, a pesar de que la falta de vuelos tierra adentro por parte de individuos no reproductivos indica que los muestreos con radar subestimarán el tamaño poblacional regional.

INTRODUCTION

The Marbled Murrelet (*Brachyramphus marmoratus*) is a threatened seabird (USFWS 1997) that flies inland to nest in the coastal old-growth forests of northwestern North America (Nelson 1997). Because of its close association with commercially valuable trees, there is great interest in counting murrelets and studying their behavior in the terrestrial environment. Murrelets generally fly inland at dawn and dusk to prospect for nests, exchange incubation duties, and provision young at sites located up to 100 km from the coast (Ralph et al. 1995). Group size for inland-flying birds varies from one to several individuals, with a mode of one to two individuals (O'Donnell et al. 1995, Jodice and Collopy 2000). Males and females share incubation duties equally, but males fly inland to provision nestlings more frequently than females (Bradley et al. 2002). Although more birds are detected inland during the breeding season, murrelets visit nesting habitat all year round in some regions (Naslund 1993).

Most of what is known about inland flight behavior of Marbled Murrelets is based on observations of unmarked birds flying above or below the canopy, and the inland flight behavior of individuals is poorly understood. Little is known about the extent that nonbreeders fly inland to prospect for nests, the level of fidelity to specific flyways, and how environmental conditions affect the frequency of inland flights. A lack of information on inland flight behavior of individual Marbled Murrelets complicates the interpretation of radar counts of birds flying inland, which have been proposed as a method to monitor Marbled Murrelets at the watershed and regional scales (Burger 2001, Cooper et al. 2001, Raphael et al. 2002).

We studied the inland flight behavior of individual Marbled Murrelets using radio-telemetry during the breeding season in central California. First, we determined how inland flight behavior varies by sex and reproductive status. Second, we estimated annual variation in the probability that an individual flew inland. Third, we estimated regional population size using at-sea surveys and estimated the proportion of breeders using radio-telemetry to determine to what extent radar surveys reflect variation in regional population size or breeding effort.

METHODS

STUDY AREA

We studied the main nesting concentration of the central California population of Marbled Murrelets in San Mateo and Santa Cruz Counties (37°06′N, 122°18′W; Carter and Erickson 1992). Marbled Murrelets in central California represent the species' southernmost breeding population, which is isolated by several hundred kilometers from the closest significant concentration of birds in northern California. The at-sea portion of the study area ranged from Half Moon Bay to Santa Cruz, California (Fig. 1). We conducted telemetry surveys for the radio-tagged murrelets using the Waddell Creek, Gazos Creek, and Scott Creek watersheds to access old-growth nesting habitat in the Santa Cruz Mountains (Fig. 1). These drainages constitute three of the five primary inland flyways used by murrelets in central California.

ASSESSING INLAND FLIGHT STATUS

We used nightlighting and dipnetting (Whitworth et al. 1997) to capture 24 Marbled Murrelets from 25 April through 16 May, 2000, and 22 murrelets from 27 April through 13 May, 2001, in Año Nuevo Bay, California. We attached radio-transmitters with a subcutaneous anchor to the back of each bird (Newman et al.

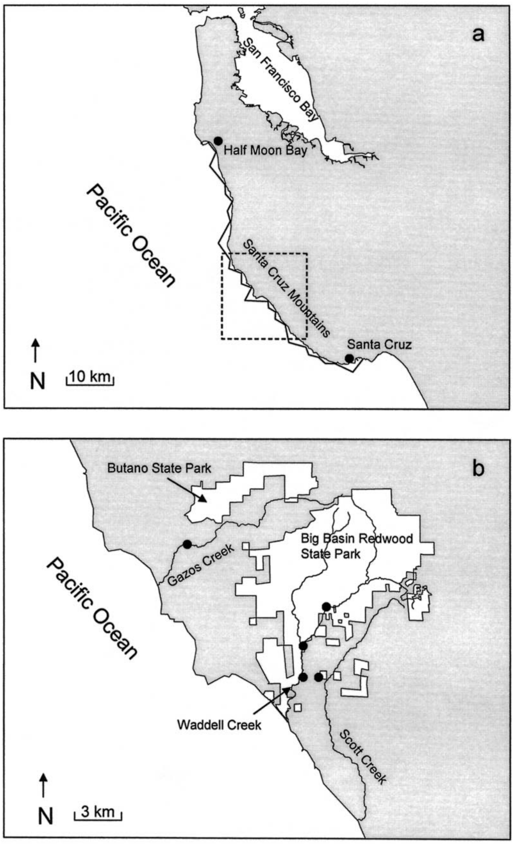

FIGURE 1. Survey stations used to track the inland flights of radio-marked Marbled Murrelets in the Santa Cruz Mountains (black dots in b) and zig-zag transect for at-sea surveys to estimate regional population size. White areas in b correspond to California State Park lands, which encompass most remaining old-growth nesting habitat.

1999; Peery et al., in press). A blood sample (1.5 mL) was taken from the medial metatarsal vein for molecular-genetic analyses to determine sex (Vanderkist et al. 1999) and to assay blood parameters that indicate breeding status.

Any radio-marked individual that was detected flying inland at least once was classified as an ''inland flyer.'' To determine which murrelets flew inland, we surveyed Waddell, Scott, and Gazos Creeks from 1 hr prior to sunrise to 1 hr after sunrise (hereafter ''inland telemetry surveys'') an average of seven times per week. We established five inland telemetry survey stations in these three drainages and on adjacent ridgetops (Fig. 1). Occasionally, when we were not able to determine if an individual was flying inland, we would conduct an inland telemetry survey exclusively for that murrelet from a location other than one of the five survey stations. To determine if a murrelet did not fly inland on a given morning, we monitored its frequency at sea from 1 hr before to 1 hr after sunrise (hereafter ''at-sea telemetry survey''). We conducted an average of six such surveys per week. During the early morning, birds were typically located at sea very near the mouth of the flyway they used to access nesting habitat. Therefore, we usually conducted paired inland and at-sea telemetry surveys where we surveyed both an inland flyway and the birds that used that flyway simultaneously. On some occasions, we were not able to conduct matching surveys and only an inland or at-sea telemetry survey was conducted. For at-sea telemetry surveys, we listened for radio frequencies from a ground-based vehicle at designated survey stations from Half Moon Bay to Santa Cruz. We monitored the frequencies of all birds audible at the beginning of the survey at 1-min intervals (i.e., the signal from each bird was monitored for 1 min before listening for the next bird). If a bird stayed on the water throughout the 2-hr period, we assumed that it did not fly inland that morning. Any bird that stayed on the water at least six mornings during the tracking period and was never heard inland was classified as a ''non-inland flyer.''

ASSESSING BREEDING STATUS

In a previous investigation of Marbled Murrelet breeding biology (Peery et al., in press), we developed three categories to characterize the reproductive status of each radio-tagged murrelet: (1) *Breeders* were birds that initiated nesting as determined by radio-telemetry; (2) *Potential breeders* were birds that did not initiate nesting but were physiologically in breeding condition at the time of capture; and (3) *Nonbreeders* were birds that did not initiate nesting and were not in breeding condition at the time of capture.

We determined if radio-marked murrelets initiated nesting by flying a fixed-wing aircraft over all potential nesting habitat in the Santa Cruz Mountains. When a bird was detected inland, we immediately visited the forested area where the signal originated to locate the nest tree. We determined nest fates by monitoring parental attendance using radio-telemetry and visual observations at the nest site. We used three physiological criteria to determine if birds were in breeding condition: (1) brood patch development (developed in both sexes; McFarlane-Tranquilla, Bradley et al. 2003); (2) plasma vitellogenin (VTG); and (3) plasma calcium (Ca). Vitellogenin is an egg-yolk precursor that becomes elevated in the plasma of female birds during egg development and is an effective indicator of breeding status for Marbled Murrelets (Vanderkist et al. 2000, Lougheed et al. 2002, McFarlane Tranquilla, Williams, and Cooke 2003). Calcium is used in eggshell formation (Newman et al. 1997) and becomes elevated in female birds during egg laying (Ivins et al. 1978). Because males do not have elevated concentrations of VTG or Ca, only non-nesting males with brood patches were considered potential breeders. Peery et al. (in press) provide a description of the assays for VTG and Ca.

ESTIMATING REGIONAL POPULATION SIZE WITH AT-SEA SURVEYS

We conducted visual surveys at-sea and used distance sampling (Becker et al. 1997, Buckland et al. 2001) to estimate the population size of Marbled Murrelets in central California in 2000 and 2001. We conducted eight surveys each in 2000 and 2001 from Half Moon Bay to Santa Cruz from a 4.5-m Zodiac along a zig-zag transect delineated from 200 to 2500 m offshore (Becker and Beissinger 2003; Fig. 1). The area surveyed encompassed >95% of the at-sea locations obtained from the radio-marked murrelets (MZP, unpubl. data) and we assumed that at-sea surveys provided a reasonable estimate of the number of Marbled Murrelets in the entire central California region. We divided the area surveyed into a nearshore stratum (200 to 1350 m from shore) and offshore stratum (1350 m to 2500 m from shore) and placed approximately three times more effort in the nearshore stratum. Surveys were conducted from 6 June through 19 August with one observer scanning on each side of the vessel. The starting point of each transect with respect to distance from shore was randomly selected such that a unique transect was followed for each survey. We recorded the number of murrelets observed in each group and their distance from the transect line by estimating the distance and angle of the group from the boat following Becker et al. (1997). Observers were trained to estimate distances and angles using floats placed at known distances from the boat for several days prior to conducting surveys and were periodically tested during the field season.

STATISTICAL ANALYSIS

We determined if breeding status of the radio-marked murrelets differed by year and if inland flight status (inland flyer or non-inland flyer) was dependent on breeding status, sex, or year using separate chi-square tests. In this analysis of inland flight behavior, we included results from all inland and at-sea telemetry surveys because the analysis depended on accurately identifying the inland flight status of each individual bird.

In a second analysis of inland flight behavior, we compared the proportion of radio-telemetry surveys that murrelets flew inland among breeding categories, years, and sexes using fixed-effects ANOVA. The proportion of surveys flown inland was calculated by dividing the number of times individuals flew inland during paired at-sea and inland telemetry surveys by the total number of paired surveys conducted. We only used results from paired inland and at-sea telemetry surveys because the objective of this analysis was to obtain an unbiased estimate of the proportion of surveys each bird flew inland. Marbled Murrelet breeding pairs have 24-hr alternating incubation shifts that begin early in the morning, so surveys for incubating individuals could only be conducted on mornings that an incubation shift was initiated. The ANOVA was conducted using PROC GLM in program SAS (SAS Institute 1990).

To determine if the frequency of inland flights changed as the breeding season progressed, we compared the proportion of telemetry surveys breeding murrelets flew inland in the prebreeding, incubation, nestling provisioning, and postbreeding stages using a chi-square test. We also compared the proportion of radio-telemetry surveys that males and females flew inland in the prebreeding stage using a chi-square test, but small sample sizes prevented us from testing for differences between sexes in any of the other stages.

We estimated the regional population size of Marbled Murrelets from the counts of individuals observed during at-sea surveys using program DISTANCE (Becker et al. 1997, Buckland et al. 2001). We modeled variation in the probability of detecting a group of murrelets as a function of distance from the transect line (i.e., the detection function) for each year separately using a half-normal key function and a cosine series expansion (Buckland et al. 2001). Previous analyses indicate that this model fits the distribution of distances for Marbled Murrelets in our region better than other models available in program DISTANCE (SRB, unpubl. data). A global detection function (i.e., common to all surveys) was modeled for each year because the number of groups observed was often too small to permit robust parameter estimation on a survey by survey basis. The probability of detecting a group was potentially affected by several factors in addition to distance, including observer and sea surface condition. Therefore, we indexed sea-surface condition by wind speed, classified as Beaufort Scale 0–1 versus Beaufort Scale 2–4 (surveys were not conducted when Beaufort Scale >4). We then analyzed observer and sea-surface condition as categorical covariates and developed four competing models for the detection function with various combinations of these effects: (1) no covariates; (2) observer; (3) sea-surface condition, and (4) sea-surface condition and observer. Competing models were ranked in terms of how well they explained variation in the distance murrelets were detected from the transect line using Akaike's Information Criterion (AIC; Burnham and Anderson 1998). We estimated the density of groups in each stratum (nearshore vs. offshore) for each survey using the best detection function model (lowest AIC score). The density of groups was then multiplied by the mean group size to estimate the density of individual murrelets. We then estimated the mean density of individuals across surveys to derive annual density estimates for each stratum. Stratum-specific density estimates were then multiplied by the area of each stratum (104.45 km^2) to obtain stratum-specific estimates of population size for each year. Population sizes for the nearshore and offshore strata were then added to estimate regional population size. All means are presented ± SE.

RESULTS

We assessed the reproductive status of 32 Marbled Murrelets, 18 in 2000 and 14 in 2001. Due to transmitter failure, 14 individuals were not tracked long enough to determine if they nested and were considered to be of unknown breeding status. Nine birds (28%) were classified as breeders, 12 birds (38%) were classified as potential breeders, and 11 birds (34%) were classified as nonbreeders. The proportion of breeders increased from 0.11 (2 of 18) in 2000 to 0.50 (7 of 14) in 2001 (Peery et al., in press).

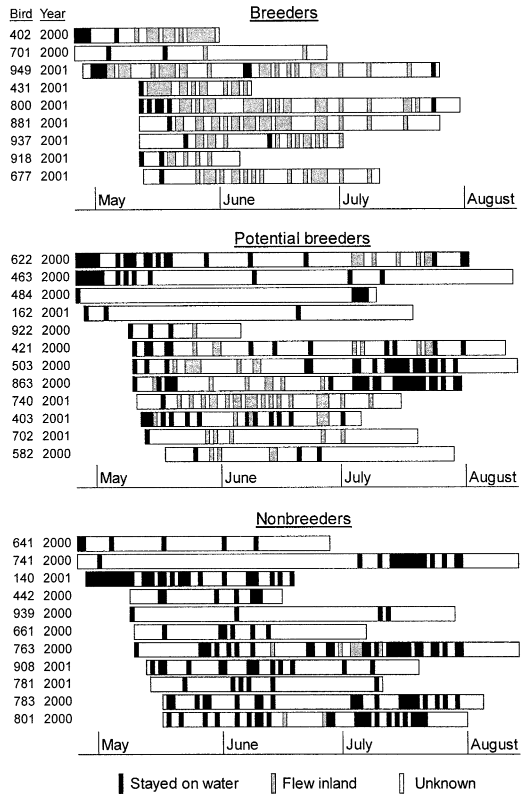

FIGURE 2. Inland flights of 32 radio-marked Marbled Murrelets of known reproductive status in central California in 2000 and 2001.

We conducted a total of 158 at-sea and 146 inland telemetry surveys in 2000 and 2001. Birds flew inland 235 times and remained on the water 378 times (Fig. 2). We characterized the inland flight status of 29 of the 32 birds of known reproductive status, of which 20 (69%) were detected flying inland at least once and were classified as inland flyers. Fifteen (75%) of the 20 inland flyers were detected using Waddell Creek, four (20%) were detected using Gazos Creek, and one (5%) was detected using Scott Creek. Each inland flyer used only a single flyway to access its nest or visit nesting habitat, except one breeder which flew up Waddell Creek (<5 km) before it flew over a ridge to attend its nest in Scott Creek.

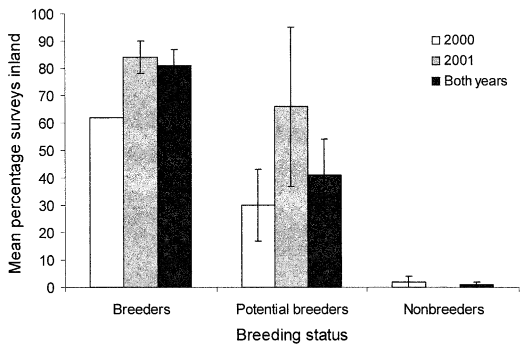

FIGURE 3. Mean ± SE percentage of surveys on which 27 radio-marked Marbled Murrelets flew inland to visit nesting habitat by breeding status and year in central California.

The percentage of birds that flew inland did not differ between 2000 (63%) and 2001 (77%; $\chi^2_1 = 0.7$, $P = 0.40$) and did not differ between males (75%) and females (62%; $\chi^2_1 = 0.6$, $P = 0.44$). However, inland flight status was dependent on breeding status ($\chi^2_2 = 17.3$, $P < 0.01$) because all breeders (100%, $n = 9$), most potential breeders (90%, $n = 10$), and few nonbreeders (20%, $n = 10$) flew inland (Fig. 2).

We estimated the proportion of times 27 Marbled Murrelets of known breeding status flew inland on 323 occasions using paired surveys (two individuals of known reproductive status were excluded because they were not located during paired surveys). The mean proportion of radio-telemetry surveys on which murrelets in all breeding categories for both years combined flew inland was 0.40 ± 0.08. The proportion of surveys on which murrelets flew inland did not differ significantly between males and females (0.38 ± 0.11, $n = 16$ and 0.43 ± 0.12, $n = 11$, respectively; $F_{1,22} = 0.4$, $P = 0.53$). The proportion of surveys on which murrelets flew inland differed among breeding categories ($F_{2,22} = 24.7$, $P < 0.01$) as breeders flew inland (0.82 ± 0.06) more often than potential breeders (0.41 ± 0.13), and potential breeders flew inland more often than nonbreeders (0.01 ± 0.01; Fig. 3). Murrelets appeared to fly inland more frequently in 2001 (0.61 ± 0.12) than in 2000 (0.20 ± 0.08), although this difference was not significant ($F_{1,22} = 2.6$, $P = 0.12$). Because Type III sums of squares were used, the difference between years was tested after accounting for variation in inland flights due to breeding status. This potentially reduced the significance of the year effect because more birds bred in 2001. When year was included in the same model without breeding status, the difference between 2000 and 2001 was highly significant ($F_{1,24} = 9.9$, $P < 0.01$). Together, breeding status and year explained 66% of the variation in proportion of occurrences that murrelets flew inland. In both years, 32% of all inland flights were made by potential breeders and nonbreeders, but the majority (70%) of inland flights were made by potential and nonbreeders in 2000 (Table 1).

TABLE 1. Proportion of inland flights made by 27 radio-marked Marbled Murrelets in three breeding categories in 2000 and 2001 in central California.

Breeding status	2000 ($n = 27$)	2001 ($n = 71$)	Both years ($n = 98$)
Breeders	0.30	0.83	0.68
Potential breeders	0.63	0.17	0.30
Nonbreeders	0.07	0	0.02

Based on 85 paired surveys of breeding murrelets, the proportion of radio-telemetry surveys individuals flew inland tended to differ among breeding stages ($\chi^2_3 = 7.2$, $P = 0.07$). Breeders in the incubation and nestling-provisioning stages flew inland during 100% of surveys ($n = 15$ and 4, respectively), while breeders in the prebreeding and postbreeding stages flew inland during 70% ($n = 43$) and 78% ($n = 23$) of surveys, respectively. All postbreeding observations were for individuals whose nests had failed. The sample size in the nestling-provisioning stage was small because only two breeding attempts did not fail during incubation.

The detection function model that best fit the distribution of distances that murrelets were observed from the transect line during at-sea surveys did not include covariates in 2000, but included both observer and viewing conditions as covariates in 2001 (Table 2). Although the best model was 2–3 times more likely to fit the data than the second best model in each year, as determined with AIC weights (Burnham and Anderson 1998), estimates of population size were similar among the competing models within years. This was particularly true in 2000 as estimates differed by only nine birds. In 2001, the model with both observer and viewing conditions differed by 57 individuals from the model without covariates. The fact that estimates were similar suggests the results are robust with respect to model structure and uncertainty. The

TABLE 2. Summary statistics for competing detection function models from at-sea surveys used to estimate population size ($\hat{N}$) of Marbled Murrelets in central California with distance sampling. AIC = Akaike's Information Criterion (Burnham and Anderson 1998), ΔAIC = the difference between the model's AIC score and the AIC score for the best model, and log(*l*) = the natural logarithm of the model's likelihood. AIC weight indicates the relative likelihood of a given model and sums to 1.

Model covariates	ΔAIC[a]	–2log(*l*)	AIC weight	No. of parameters	$\hat{N}$	95% CI
2000						
No covariates	0	1617.17	0.56	1	496	338–728
Sea surface	1.97	1617.14	0.21	2	496	339–728
Observer	2.46	1615.63	0.17	3	499	340–731
Sea surface + Observer	4.42	1623.59	0.06	4	490	340–731
2001						
Sea surface + Observer	0	605.23	0.69	4	637	441–920
Sea surface	2.35	609.58	0.21	2	625	433–902
Observer	4.08	611.32	0.09	3	625	433–902
No covariates	13.30	624.53	<0.01	1	580	418–805

[a] Lowest AIC scores were 1619.17 for 2000 and 613.23 for 2001.

difference in model rankings between years was partially due to differences in abilities of observers, but it is unclear why there was no effect of viewing condition in 2000.

Using the best detection function model in each year, we estimated that the regional population size of Marbled Murrelets was 496 (95% CI = 338–728, $n = 8$ surveys) in 2000 and 637 (95% CI = 441–920; $n = 8$ surveys) in 2001, a 28% increase. Confidence intervals were large, and the high degree of overlap indicated the change in population size was not significant. In contrast, the proportion of breeders increased by 355% and the mean proportion of times individual birds flew inland increased 205% during the same period (Table 3).

DISCUSSION

We observed a clear difference in inland flight behavior among non-nesting Marbled Murrelets, as potential breeders frequently flew inland but nonbreeders rarely flew inland. Some nonbreeders could have been below the age of first breeding (3–4 years; De Santo and Nelson 1995) and had not yet begun prospecting for nest sites. In fact, two nonbreeders that did not fly inland were only one year old (i.e., were banded as juveniles the year prior to radio-tagging). Individuals below the age of first breeding for other species of alcids, such as Thick-billed Murres (*Uria lomvia*; Gaston and Nettleship 1981) and Cassin's Auklets (*Ptychoramphus aleuticus*; Ainley et al. 1990), often do attend nesting colonies and it is unlikely that age is the only reason that nonbreeding Marbled Murrelets did not fly inland. Consequently, many nonbreeders may have been mature birds that were unable to procure sufficient resources to initiate breeding and had forgone attending potential nest sites. Prey availability was apparently reduced in 2000, when a high proportion of birds did not nest or fly inland, based on observations of foraging behavior (Peery et al., in press). Nonbreeders were unlikely to be limited by nest-site availability because they did not fly inland to prospect for nests (Peery et al., in press).

TABLE 3. Change in population parameters for Marbled Murrelets in central California from 2000 to 2001. Breeding and inland flight behavior variables estimated with radio-telemetry; population size estimated with at-sea surveys.

Population parameter	2000	2001	% Change
Proportion of breeders	0.11	0.50	355
Mean probability of flying inland	0.20	0.61	205
Proportion of flights by non-nesters	0.70	0.17	–312
Population size	496	637	28

Female potential breeders with elevated levels of VTG and Ca ($n = 4$) probably flew inland to attend nest sites that they had already selected because they had advanced to the egg-building stage at the time of capture. It is possible that some potential breeders had nests that failed prior to radio-tagging and flew inland as they attempted to renest. However, of the 12 potential breeders, 6 were males that had a brood patch and 2 were females that had a brood patch but not elevated VTG or Ca. The presence of a brood patch only indicates that some of the hormonal changes associated with breeding have occurred and does not necessarily indicate that egg-building or incubation has been initiated (McFarlane Tranquilla, Bradley et al. 2003). Moreover, at-sea surveys indicated that trapping and radio-tagging was initiated immediately (<5 days) following the beginning of the arrival of murrelets to at-sea areas adjacent to nesting habitat and all birds were captured within 3 weeks of arrival (MZP, unpubl. data). Most breeders did not initiate nesting until several weeks after radio-tagging (mean ± SE: 30 ± 5.4 days, range 0–43 days), indicating that females with elevated VTG and Ca probably did not have time to build an egg, lay it, experience nest failure, and then begin developing a second egg prior to radio-tagging. This is particularly true because egg building is believed to take at least 14 days and VTG appears to decline to baseline levels following egg-laying for Marbled Murrelets (McFarlane Tranquilla et al., in press), and renesting murrelets should not have elevated VTG until they started building their replacement egg (Challenger et al. 2001, Salvante and Williams 2002). Rather, it seems more likely that females were building their first egg at the time of capture than their replacement egg. Finally, it is unlikely that radio-marked birds nested without being detected during the study period because we located potential breeders and nonbreeders at sea almost every day while radio-transmitters were functioning. Radio-tagging could have caused some potential breeders to abandon their nests, but the proportion of breeders in this study was estimated to be much lower than in Desolation Sound, British Columbia, Canada, using similar techniques, suggesting that environmental factors prevented some birds from breeding in central California (Peery et al., in press).

Murrelets visited nest sites every morning during incubation and nestling provisioning, but visitation was lower during the pre- and post-breeding stages when they were not tied to an active nest. Perhaps the benefit of saving energy by sometimes remaining at sea outweighed the benefit of attending a nest site on all mornings during the prebreeding period. The function of inland flights in the postbreeding period is uncertain, but some individuals may have continued to fly inland in an attempt to renest. We did not detect a difference in the frequency of inland flights between males and females in the prebreeding stage. Although we were unable to test for differences in any of the other three stages, males fly inland in British Columbia more often than females to feed nestlings (Bradley et al. 2002). Nevertheless, there is no reason to expect differences in inland flight behavior between sexes during the incubation stage because males and females share incubation duties equally.

IMPLICATIONS OF INLAND FLIGHT BEHAVIOR FOR MONITORING

An important objective for radar-based monitoring studies of Marbled Murrelets will be to index or estimate the number of individuals using a watershed or set of watersheds, especially as it relates to harvest history and the amount of available old-growth forest (Burger 2001, Raphael et al. 2002). The fact that radio-marked murrelets were faithful to specific flyways is encouraging for radar-based monitoring, particularly at the watershed scale. High site-fidelity within years should reduce among-survey variance and lessen the likelihood that changes in numbers of murrelets using a flyway will mistakenly be attributed to changes in numbers in other watersheds. However, fidelity to flyways among years is uncertain in our study because we did not radio-mark the same birds in both years.

The increase in the frequency of inland flights between years in this study clearly reflected a change in breeding effort (i.e., breeding population size), rather than a change in regional population size, because we observed only a relatively small, nonsignificant increase in number of birds based on at-sea surveys from 2000 to 2001. Even though confidence intervals for population size estimated by at-sea surveys were large, a threefold increase is improbable because murrelets have a clutch size of one (Nelson 1997), reproductive success in the region is low (Peery et al., in press), and intrinsic rates of increase are low (Beissinger 1995). Large annual variation in inland flights due to fluctuations in breeding effort will increase the number of years needed to detect population declines with radar (Cooper et al. 2001).

Radar cannot differentiate between breeders, potential breeders, and nonbreeders, and 30% of all inland flights were made by individuals in the latter two categories (potential breeders = 28% and nonbreeders = 2%). Thus, our results suggest that counts from radar surveys can overestimate breeding population size due to regular inland flights by potential breeders and underestimate regional population size because nonbreeders rarely fly inland and not all individuals nest or fly inland in unfavorable years. Moreover, the percentage of all inland flights made by potential breeders was much higher in 2000 than in 2001 (63% versus 17%) indicating that the magnitude of biases in population estimates can vary among years. Consequently, we suggest that inferences from radar counts of Marbled Murrelets should be limited to indices of the size of the *potential* breeding population and not to breeding or regional population size. This index will fluctuate annually due to variation in breeding effort that is likely driven both by marine conditions and factors in the terrestrial environment. Nevertheless, if conducted over a long period, radar surveys should detect gradual declines in breeding population size due to loss of nesting habitat because the maximum number of individuals that can nest will decline.

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