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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 chickincremento 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

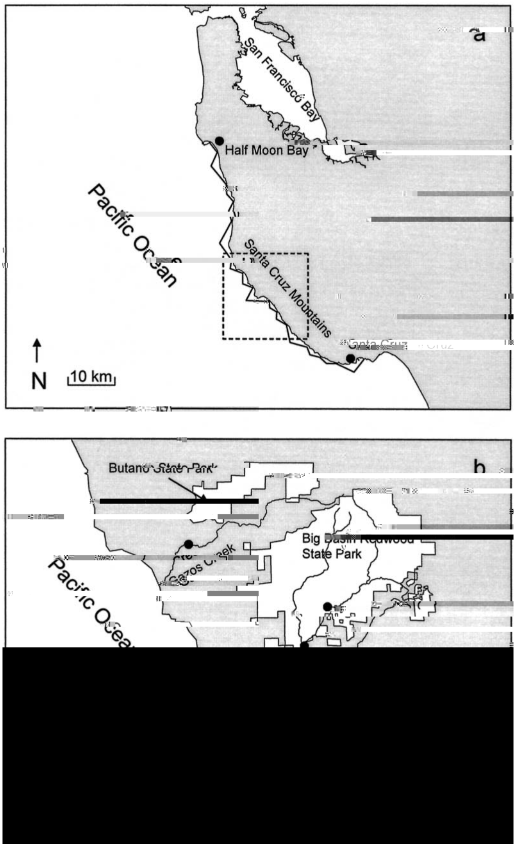

FIGURE 1. Survey stations used to track the inland flights of radio-marked Marbled Murrelets in the Santa Cruz Mountains (black dots in b) and zig-zag transect for at-sea surveys to estimate regional population size. White areas in b correspond to California State Park lands, which encompass most remaining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

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 6 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).

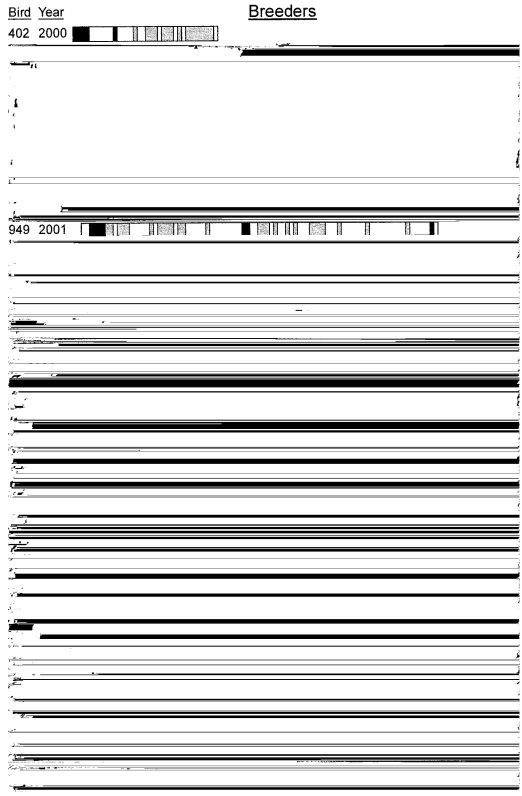

FIGURE 2. Inland flights of 32 radio-marked Marbled Murrelets of known reproductive status in central California in 2000 and 2001.

We conducted a total of 158 at-sea and 146

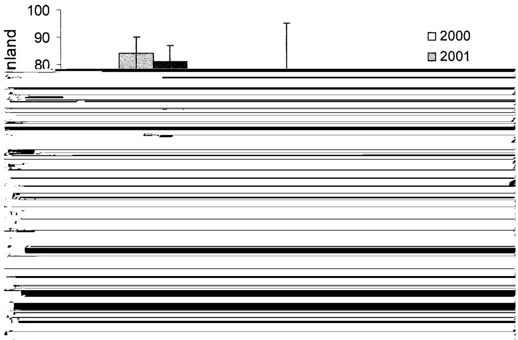

FIGURE 3. Mean ± SE percentage of surveys on which 27 radio-marked Marbled Murrelets flew inland to visit nesting habitat by breeding status and year in central California.

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

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).

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 es-

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 5 Akaike's Information Criterion (Burnham and Anderson 1998), DAIC 5 the difference between the model's AIC score and the AIC score for the best model, and log(*l*) 5 the natural logarithm of the model's likelihood. AIC weight indicates the relative likelihood of a given model and sums to 1.

Model covariates	DAIC[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 1 Observer	4.42	1623.59	0.06	4	490	340–731
2001						
Sea surface 1 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 5 338–728, *n* 5 8 surveys) in 2000 and 637 (95% CI 5 441–920; *n* 5 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*

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* 5 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 6 SE: 30 6 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 crease 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 5 28% and nonbreeders 5 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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