Applying the Declining Population Paradigm: Diagnosing Causes of Poor Reproduction in the Marbled Murrelet

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Abstract: *We identified six approaches to diagnosing causes of population declines and illustrate the use of the most general one ("multiple competing hypotheses") to determine which of three candidate limiting factors—food availability, nesting site availability, and nest predation—were responsible for the exceptionally poor reproduction of Marbled Murrelets (* Brachyramphus marmoratus*) in central California. We predicted how six attributes of murrelet demography, behavior, and physiology should be affected by the candidate limiting factors and tested predictions with field data collected over 2 years. The average proportion of breeders, as estimated with radiotelemetry, was low (0.31) and varied significantly between years: 0.11 in 2000 and 0.50 in 2001. Murrelets spent significantly more time foraging in 2000 than in 2001, suggesting that low food availability limited breeding in 2000. In 2001, 50% of radio-marked murrelets nested and 67% of females were in breeding condition, suggesting that enough nest sites existed for much of the population to breed. However, rates of nest failure and nest predation were high (0.84 and 0.67–0.81, respectively) and few young were produced, even when a relatively high proportion of murrelets bred. Thus, we suggest that reproduction of Marbled Murrelets in central California is limited by food availability in some years and by nest predation in others, but apparently is not limited by availability of nesting sites. The multiple-competing-hypotheses approach provides a rigorous framework for identifying causes of population declines because it integrates multiple types of data sets and can incorporate elements of other commonly used approaches.*

Key Words: conservation, demography, declining population paradigm, Marbled Murrelet, population declines, reproductive success

Aplicación del Paradigma de la Población en Disminucioń: Diagnosis de las Causas de la Reproducción Deficiente de *Brachyramphus marmoratus*

Resumen: *Identificamos seis métodos utilizados para diagnosticar las causas de la disminucioń de poblaciones y damos un ejemplo del uso del más general ("hipótesis de competencia múltiple") para determinar cual de tres posibles factores limitantes (disponibilidad de alimento, disponibilidad de sitios de anidación y depredación de nidos) es responsable de la reproducción excepcionalmente deficiente de* Brachyramphus marmoratus *en California central. Predijimos el efecto de los factores limitantes sobre seis atributos de la demografía, comportamiento y fisiología de* B. marmoratus*, y probamos las predicciones con datos de campo recolectados a lo largo de 2 años. La proporción promedio de reproductores, estimada con radiotelemetría, fue baja (0.31) y varió significativamente entre años: 0.11 en 2000 y 0.50 en 2001.* B. marmoratus *forrajeó*

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significativamente más tiempo en 2000 que en 2001, lo que sugiere que la baja disponibilidad de alimento limitó la reproducción en 2000. En 2001, 50% de los individuos radio-marcados anidó y 67% de las hembras estaban en condición reproductiva, lo que sugiere que existían suficientes sitios para nidos para la reproducción de la mayorí

Table 1.

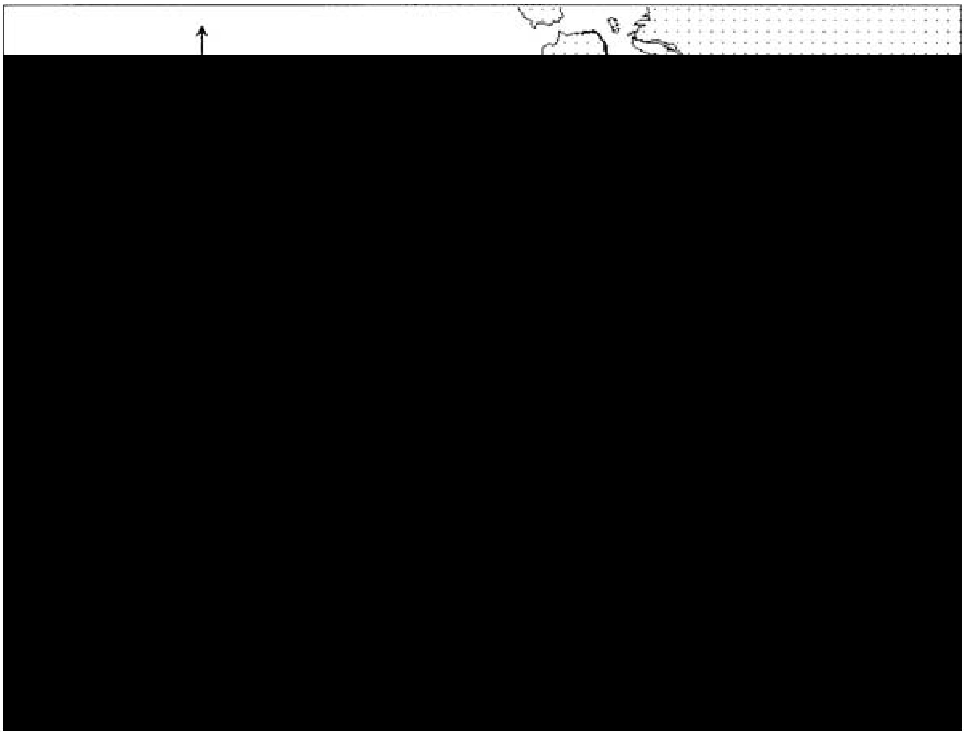

Figure 1. Map of study area, scanning stations used to determine which radiomarked Marbled Murrelets flew inland to visit nesting habitat (black dots), and at-sea transect for estimating the juvenile ratio for Marbled Murrelets (zig-zag line).

for nest sites. Moreover, few individuals should be physiologically preparing to breed if nest sites were limiting because elevated blood chemistry parameters suggest that egg building has begun (Farner & Gwinner 1980; Wingfield 1980; McFarlane-Tranquilla et al. 2003*a*). If nest predation limited reproductive success, both the rate of nest failure and the proportion of breeders would be high. We also predicted that a high proportion of individuals would fly inland to visit nest sites and would be in breeding condition.

If food availability limited reproduction, the proportion life of 12–16 weeks. Radiotelemetry units were attached with the subcutaneous anchor technique (Newman et al. 1999). We administered a mild inhalation anesthetic, Isoflurane, to facilitate handling in 2000 but not in 2001. Anesthesia should not have affected breeding behavior

Table 4. Effect of breeding status, year, and time of day on the proportion of time Marbled Murrelets spend diving, determined by a mixed-model analysis of variance.

Effect	*df*	f	p
Year	1,29	5.24	0.03
Breeding status	2,27	0.07	0.93
Time of day	1,30	0.01	0.98
Breeding status × time of day	2,28	2.60	0.09
Time of day × year	2,27	1.55	0.23
Breeding status × year	2,25	0.50	0.61

have caused failure at 7 additional nests, however, resulting in a maximum predation rate of 0.81 (SE = 0.10).

Inland Flights and Foraging Effort

We conducted 156 at-sea and 141 inland surveys to assess the inland flight status of 29 birds of known reproductive status. Twenty individuals (62%; SE = 0.09) were detected flying inland at least once. All breeders ($n = 9$), 90% of potential breeders ($n = 10$), but only 20% of nonbreeders ($n = 10$) flew inland (Peery et al. 2004).

We conducted 700 hour-long dive surveys for 31 individual murrelets. Murrelets spent a significantly greater proportion of time diving in 2000 (mean = 0.126, SE = 0.006) than in 2001 (mean = 0.096, SE = 0.007) (Table 4). This difference was consistent among breeding categories (Fig. 3).

Fecundity Estimates

With the proportion of breeders estimated in this study (0.31), the rate of nest success based on all the nests located in the region (0.16), and the assumption that 93% of the radiomarked birds were old enough to breed based on Beissinger's (1995) model, fecundity was estimated at 0.027. The mean juvenile ratio from at-sea surveys in 2000

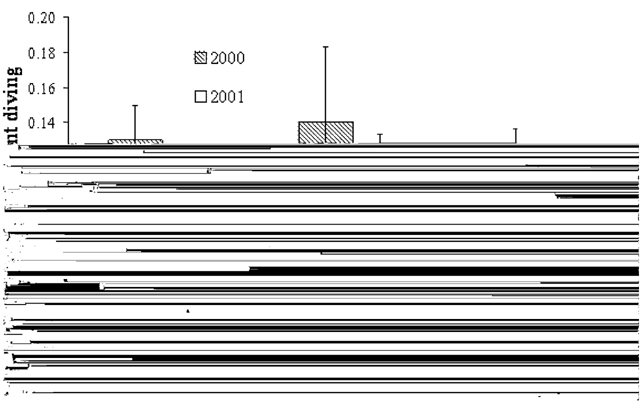

Figure 3. Mean proportion of time spent diving (±95% confidence interval) by Marbled Murrelets of three different breeding categories in 2000 (hatched) and 2001 (white).

was 0.021 (SE = 0.017, $n = 7$ surveys) and in 2001 was 0.040 (SE = 0.029, $n = 6$ surveys), from which fecundity was estimated as 0.029 (SE = 0.016) in 2000 and 0.055 (SE = 0o/MC690wacgC2asfecundity

2000 and likely affected breeding in other years. Only 50% of murrelets nested in 2001, a relatively low proportion (Bradley et al., 2004), although additional years of study might detect a greater proportion. Both fishing and climate change have apparently lowered the trophic level at which murrelets feed (Becker 2001). Reduced quotas for small, commercially harvested prey fishes, which are important murrelet food items (Burkett 1995; Becker 2001), may be needed to increase murrelet productivity.

The nest-predation hypothesis was supported by a high rate of nest failure (84%) due primarily to predation (67–81%), a high proportion of birds in breeding condition, and a high proportion of birds flying inland. Because nest predation was observed so frequently, particularly by Steller's Jays (*Cyanocitta stelleri*) and Common Ravens (*Corvus corax*), it also limits murrelet reproduction. Thus, our results suggest that murrelet reproduction is too low to maintain a stable population because low food availability prevents many birds from nesting in some years and because high levels of nest predation occurred in years when more birds nested. Current nesting habitat in central California is largely restricted to campgrounds in state parks, where handouts from campers attract corvids, and corvid populations have increased greatly throughout the region since 1966 (Liebezeit & George 2002). Relocating campgrounds away from old-growth nesting habitat might reduce nest predation.

Support for the nest-limitation hypothesis was ambiguous. As predicted, the proportion of breeders was low, and non-nesting birds flew inland regularly. Contrary to predictions, many non-nesting birds were in breeding condition (i.e., potential breeders), and annual variability in murrelet attributes was high. Did a lack of nest sites cause half the murrelets not to lay eggs in 2001? Females with elevated plasma vitellogenin or calcium levels should have already selected nest sites because they had initiated egg building (Vanderkist et al. 2000; Lougheed et al. 2002*b*; McFarlane-Tranquilla et al. 2003*a*), even though they did not initiate incubation (the relationship between brood patch and incubation status is unclear; McFarlane-Tranquilla et al. 2003*a*). Supplementary cues, such as the presence of a mate and a nest site, are believed to be required to stimulate ovary development (Farner &

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Appendix 1. Fates of 19 Marbled Murrelet nests in the Santa Cruz Mountains, California.

					Failure		
Nest site name	*Easting UTM*	*Northing UTM*	*Year*	*Fate*	*stage*[a]	*cause*[b]	*Source*
Sempervirens Creek	570102	4115527	2001	failed	N	unknown, not predated	this study
Opal Creek #2	569642	4114459	2001	failed	I	unknown, possible predation	this study
East Fork Waddell #1	568652	4113099	2001	failed	I	unknown, possible predation	this study
East Fork Waddell #2	568619	4112982	2001	failed	I	nonviable egg	this study
Blooms Creek Campground #1	569737	4113368	2001	failed	I	unknown, possible predation	this study
Scott Creek	568000	4109600	2001	failed	N	predated by raptor	this study
Butano State Park	563210	4120420	2000	failed	I	abandoned	this study
Blooms Creek Campground #2	569480	4113390	2002	failed	N	predated by CORA	D. Suddjian, unpublished data
Lair Gulch	566110	4105950	1997	failed	N	unknown, possible predation	E. Burkett, unpublished data
Portola State Park	570420	4121800	1997	failed	I	predated by RSHA[c]	E. Burkett, unpublished data
Berry Creek Falls	565380	4113810	1997	failed	I	unknown, possible predation	E. Burkett, unpublished data
Lesk Tree	569050	4114090	1996	successful	—	—	E. Burkett, unpublished data
Father Tree #4	569080	4113830	1996	failed	I	unknown, possible predation	S. Singer, unpublished data
Hidden Gulch	561290	4123690	1995	failed	I	predated by CORA	D. Suddjian, unpublished data
Father Tree #3	569080	4113830	1994	failed	U	unknown, possible predation	Singer et al. 1995
Father Tree #2	569080	4113830	1992	successful	—	—	Singer et al. 1995
Father Tree #1	569080	4113830	1991	successful	—	—	Singer et al. 1995
Waddell Creek	568600	4113220	1989	failed	N	predated by STJA	Singer et al. 1991
Opal Creek #1	569170	4114310	1989	failed	I	predated by CORA	Singer et al. 1991

[a] *I, incubation; N, nestling; U, unknown.*
[b] CORA
1992 successful