
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 Disminución: Diagnóstico de las Causas de la Reproducción Deficiente de *Brachyramphus marmoratus*

Resumen: *Identificamos seis métodos utilizados para diagnosticar las causas de la disminución 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 radiotelegrafía, 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 mayoría de la población. Sin embargo, las tasas de fracaso y depredación de nidos fueron altas (0.84 y 0.67–0.81, respectivamente) y se produjeron pocos juveniles, aun cuando haya criado una proporción relativamente alta de adultos. Por tanto, sugerimos que la reproducción de *B. marmoratus* en California central está limitada por la disponibilidad de alimento en algunos años y por la depredación de nidos en otros, pero aparentemente no está limitada por la disponibilidad de sitios de anidación. El método de la hipótesis de competencia múltiple proporciona un riguroso marco de referencia para identificar causas de la declinación de poblaciones porque integra conjuntos de datos de múltiples tipos y puede incorporar elementos de otros métodos comúnmente utilizados.

Palabras Clave: *Brachyramphus marmoratus*, conservación, declinaciones poblacionales, éxito reproductivo, paradigma de la población declinante

Introduction

Identifying factors responsible for population declines is essential for designing a management strategy that will recover an endangered species. Caughley (1994) proposed a framework for identifying such factors, known collectively as the “declining population paradigm,” which involves confirming that the population has declined, determining which demographic parameters are depressed, identifying potential causes of decline through natural-history investigations, and experimentally manipulating candidate limiting factors. Experimentation provides a powerful means of disentangling the effects of multiple potential causes of decline (Cooper & Walters 2002; Yates & Broadhurst 2002), but many endangered species and the factors that threaten them are not amenable to manipulation (Green 2002).

Five alternative approaches have been used to identify causes of decline that vary considerably in methodology, data requirements, and scale (Table 1). First, an expected demographic response can be modeled for each potential cause and compared with independently collected population data (modeled population response; Pascual & Adkinson 1994). This approach is more exploratory than explanatory because it does not incorporate explicit information on the causes of decline and because modeled mechanisms are rarely confirmed. Second, rates of decline can be compared among populations experiencing different environmental conditions (population comparisons approach; Green & Hirons 1991; Green 1995, 2002). This is potentially a powerful approach, but endangered species are often restricted to one or a few populations, resulting in small sample sizes. Moreover, different factors may limit different populations. Third, each species in a set of related species is placed into a life-history category and rates of decline are compared among categories (species life-history comparisons approach; Böhning-Gaese et al. 1993; Lips 1998; Davies et al. 2000). Although this approach can provide insight into factors affecting a set of species, it does not necessarily

identify causes of decline for a species of interest. Fourth, the timing of a population decline can be related to the timing of changes in candidate limiting factors (timing of decline approach; Green 1995, 2002; McCulloch & Norris 2001; Stallard 2001). Such an approach is powerful but often not feasible because accurate population data for periods prior to a decline are rarely available. All of the above approaches can potentially provide useful insights into causes of population declines, but can only be applied in specific situations and do not necessarily identify causal mechanisms.

Caughley and Gunn (1996) mentioned a sixth approach that involves developing a series of competing predictions about the effects of each factor on the behavior, habitat use, demography, and trophic interactions of a species of interest and then designing field studies to test the predictions. This process, which we call the “multiple competing hypotheses” approach (MCH), is perhaps the most general approach for diagnosing causes of population declines and can incorporate elements from other approaches in the predictions. The MCH is an approach to strong inference commonly used in other sciences (Popper 1959; Platt 1964). Although it resembles the information-theoretic approach to model selection of Burnham and Anderson (2002), in MCH multiple data sets are evaluated against predictions from multiple limiting factors, whereas the method of Burnham and Anderson fits multiple candidate models to one data set. Like other approaches, MCH may not necessarily separate causation from correlation. However, by employing multiple, independent measures to develop predictions and by looking for concordance of results, it may be possible to conclude that some limiting factors are more important than others. There are few clear applications of this approach (c.f. Savidge 1987), despite its generality and potential to identify causes of population declines.

We applied the MCH to determine the causes of population declines in the Marbled Murrelet (*Brachyramphus marmoratus*; family: *Alcidae*) in central California. By implementing the MCH approach for this exceptionally

Table 1. Comparison of six approaches used to determine the causes of population declines for threatened species.

<i>Approach</i>	<i>Methodology</i>	<i>Data required*</i>	<i>Spatial scale</i>	<i>Limitations</i>
Experimentation	manipulate candidate factors and measure demographic response	P or D, E or B	generally small	feasibility, limited scale
Modeled population response	compare modeled population with population data	P, D	small to large	environmental or behavioral data not incorporated
Population comparisons	compare demographics of populations in different environments	P or D, E	large	data from multiple populations required
Species life-history comparisons	compare demographics of species with different life histories and susceptibilities	P or D, LH or B	large	cause of decline for individual species unknown
Timing of decline	compare environmental variables before and after population decline	P or D, E	small to large	data prior to decline required
Multiple competing hypotheses	test competing predictions of candidate environmental factors with field data	P or D, E or B	generally small	unique predictions required, limited scale

*P, population; D, demographic; E, environmental; LH, life history; B, behavioral.

challenging species, we hope to motivate others to develop rigorous hypotheses and field studies that test explicitly which factors are responsible for declines in other threatened species. This federally threatened seabird (USFWS 1997) lays a single egg in nests located primarily in coastal old-growth forests in the Pacific Northwest, Canada, and Alaska. Its secretive behavior made its nest among the last to be found among North American birds (Nelson 1997). Moreover, few murrelets were caught prior to the development of a logistically challenging capture technique (Whitworth et al. 1997). Extensive harvesting of old-growth forests is considered to have greatly reduced Marbled Murrelet populations, but other threats include oil spills, gillnetting, declines in prey availability, and increases in nest predator populations such as corvids and raptors (Carter & Erickson 1992; USFWS 1997; Becker 2001).

The effectiveness of potential management options is unknown because causes of decline have not been clearly determined. Two lines of evidence, however, suggest that low reproduction is causing Marbled Murrelet population declines. First, adult survival rates (Cam et al. 2003; M.Z.P., unpublished data) are similar to predictions from comparative analyses of other alcids (Beissinger 1995; Beissinger & Nur 1997). Second, the ratio of juveniles (young of the year) to after-hatch-year birds (≥ 1 year old)—hereafter, “juvenile ratio”—near the end of the breeding season is low (0.01–0.09) throughout the Pacific Northwest (Beissinger & Nur 1997). Population models suggest that stable murrelet populations require juvenile ratios between 0.18 and 0.28, and fecundity levels between 0.20 and 0.46 (Beissinger & Nur 1997). Although the accuracy of juvenile ratios has been questioned (Lougheed et al. 2002a), the exceptionally low number of juveniles observed at sea strongly suggests

that reproductive success is too low to support a viable population.

We used MCH to assess the importance of three limiting factors—food availability, nesting site availability, and nest predation—potentially responsible for the low reproductive success of Marbled Murrelets. We developed a suite of competing predictions relating to murrelet attributes, including demographic (proportion of breeders and rate of nest failure), behavioral (inland flight behavior and foraging effort), and physiological (presence of a brood patch and two blood chemistry parameters that become elevated prior to egg laying) attributes, and then looked for concordance of results (Table 2).

If a lack of suitable nest sites limited reproductive success, the proportion of breeders should be low and a high proportion of nonbreeders should fly inland to prospect

Table 2. Predicted effects on demographic, physiological, and behavioral attributes of three hypothetical environmental factors limiting the reproductive success of Marbled Murrelets.

<i>Attribute</i>	<i>Factor limiting reproductive success</i>		
	<i>nesting habitat</i>	<i>nest predation</i>	<i>food availability</i>
Proportion of breeders	low	high	low
Proportion of birds in breeding condition*	low	high	low or high
Nest failure rate	no effect	high	high
Proportion of birds flying inland	high	high	low or high
Foraging effort	no effect	no effect	high
Annual variation in attributes	low	low	high

*As determined by elevated levels of plasma calcium and vitellogenin and the presence of a brood patch.

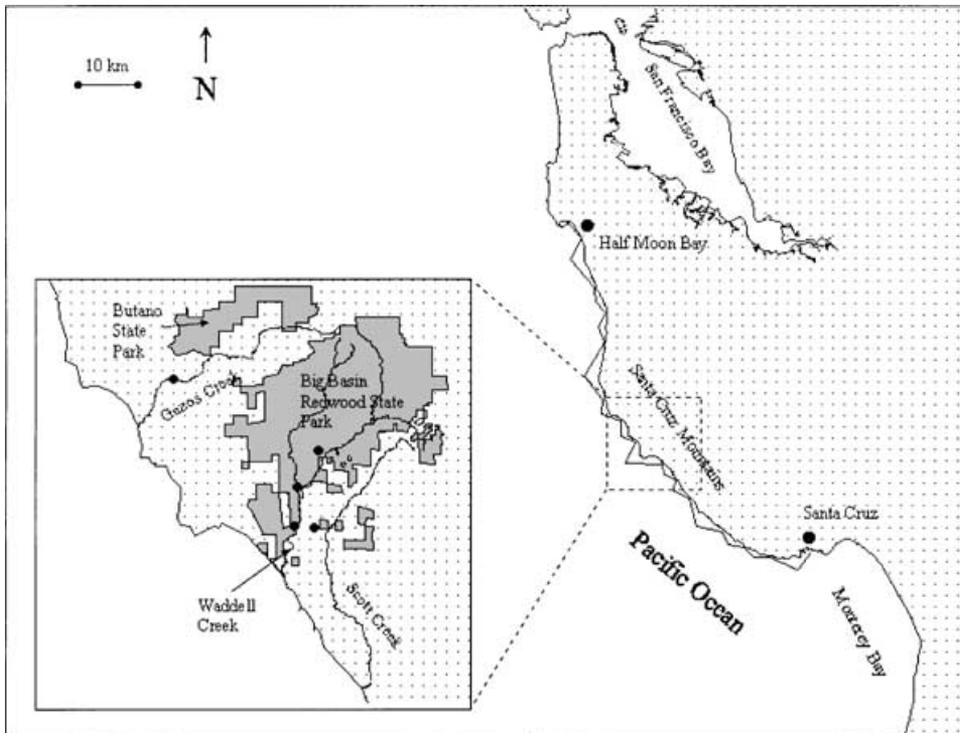


Figure 1. Map of study area, scanning stations used to determine which radiomarked Marbled Murrelets flew inland to visit nesting habitat (black dots), and at-sea transect for estimating the juvenile ratio for Marbled Murrelets (zig-zag line).

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. 2003a). 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 of breeders would be low, the rate of nest failure would be high, and the amount of time individuals spend foraging would be high. The effect of food limitation on the proportion of birds flying inland and the proportion of birds in breeding condition is less clear. In bad years, individual murrelets may not achieve breeding condition or visit nesting habitat. In years when prey is moderately reduced, individuals may still fly inland and exhibit breeding condition without initiating a nest.

Finally, we predicted that annual variation in murrelet attributes would differ among potential limiting factors. Prey availability varies considerably on an annual basis as a result of El Niño events and other oceanographic factors in central California (Becker & Beissinger 2003). Consequently, we predicted high annual variability in murrelet demographic, behavioral, and physiological attributes if prey availability limited reproductive success in some years and not in others (Table 2). In contrast, the amount of nesting habitat and the size of nest predator populations changed relatively little during our study, so we pre-

dicted that attributes would exhibit relatively little annual variation if these factors limited reproduction.

Methods

Study Area

We studied the main nesting concentration of the central California population of Marbled Murrelets in San Mateo and Santa Cruz counties, California (Carter & Erickson 1992). The inland portion of our study area encompassed areas of old-growth forest in the Santa Cruz Mountains, and the at-sea portion ranged from Half Moon Bay to Santa Cruz, California (Fig. 1).

Estimating the Proportion of Breeders and the Rate of Nest Failure: Captures, Radiotagging, and Radiotracking

From a 3-m inflatable boat, we used the "night-lighting/dip-netting" technique (Whitworth et al. 1997) to capture 24 Marbled Murrelets from 25 April through 16 May 2000 and 22 murrelets from 27 April to 13 May 2001 in Año Nuevo Bay, California. We banded and scored murrelets for the degree of brood patch development (Sealy 1972). 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 indicators of breeding status. Radio transmitters were made by Holo-hil Systems (model BD-2G), weighed 2.2 g (approximately 1.0% of murrelet body mass), and had an expected radio

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 because (1) anesthetized murrelets recovered in <10 minutes with no noticeable effects on reflexes, vigor, respiration, body temperature, or behavior (Newman et al. 1999) and (2) all birds that nested except one did so more than a month after capture. Had anesthesia prevented birds from breeding in 2000, we would have expected birds to commence nesting immediately after capture in 2001, which they did not.

We tracked radiomarked murrelets with aerial and ground-based telemetry from four-wheel-drive vehicles outfitted with a null-peak antenna arrangement (Kenward 1987). We attempted to obtain one location per 24-hour period for each murrelet. If a radiomarked murrelet was not located at sea, we flew over all potential nesting habitat in the region to locate incubating birds (Fig. 1). When a bird was detected inland, we immediately visited the area where the signal originated to locate the nest tree and returned early the following morning to observe the pair exchanging incubation duties to pinpoint the nest site. We determined nest fates and causes of failure by monitoring parental attendance with radiotelemetry and visual observations at the nest site. A nest was classified as conclusively depredated if predation was observed directly. When parents stopped attending the nest prior to the expected fledging date (54–70 days after the initiation of incubation; Nelson & Hamer 1995a), we climbed the nest tree to confirm failure and evaluate the cause. If an intact egg or chick was not located during these climbs, we considered predation a possible cause of failure. A juvenile was considered to have fledged successfully if its parents attended the nest regularly until the expected fledging date or if it was observed leaving the nest. We calculated nest success as the number of successful nests divided by the number of nests found.

Assessing Breeding Status

We developed three categories to characterize the reproductive status of radiomarked murrelets: (1) breeders, birds observed nesting; (2) potential breeders, birds that did not initiate nesting but were physiologically in breeding condition; and (3) nonbreeders, birds that did not initiate nesting and were not in breeding condition. A murrelet was classified as not nesting if it was not observed incubating and was regularly located at sea from the time of capture until 5 July, when 90% of nests should have been initiated (Hamer & Nelson 1995; M.Z.P., unpublished data). Birds that did not nest and whose radios failed prior to 5 July were considered to be of unknown breeding status and were excluded from further analyses.

We used three physiological criteria to determine whether birds were in breeding condition: (1) brood patch development (developed in both sexes; McFarlane-Tranquilla et al. 2003b), (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. 2002b; McFarlane-Tranquilla et al. 2003a). Calcium is used in egg-shell formation (Newman et al. 1997) and becomes elevated in females 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. We measured levels of vitellogenic zinc to estimate plasma VTG (Mitchell & Carlisle 1991; Vanderkist et al. 2000). To assay Ca, we used standard enzymatic rate reactions (Newman et al. 1997). Any female with a brood patch, VTG levels greater than the mean male level plus 3 SD (0.64 $\mu\text{g}/\text{mL}$ VTG, $n = 26$), or Ca levels greater than the mean male level plus 3 SD (9.97 mg/dL CA, $n = 26$) was considered to have initiated egg building and to be in breeding condition.

Sampling Inland Flight Behavior and Foraging Effort

To determine which birds flew inland, we surveyed three inland flight routes used by murrelets from 1 hour prior to sunrise to 1 hour after sunrise from five scanning stations up to six times per week (Fig. 1). To determine whether a murrelet did not fly inland on a given morning, we monitored its frequency at sea from 1 hour prior to and 1 hour after sunrise. Murrelets that remained at sea throughout this period were assumed not to have flown inland that morning. Birds that stayed on the water at least six times and were never heard inland were assumed not to have flown inland during that breeding season.

We estimated how much time radiomarked murrelets spent diving (i.e., actively foraging) based on signal quality from the radiotransmitters, because signals are not audible when radiomarked birds dive below the surface to pursue prey (Wanless et al. 1988; Jodice & Collopy 1999). We conducted 1-hour “dive surveys” from ground-telemetry vehicles, during which we tallied the number of dives and the duration of each dive. We conducted dive surveys daily from 0500 to 2100 hours and randomized the order in which murrelets were sampled. We used mixed-model analysis of variance (Littell et al. 1996) to compare the mean proportion of time spent diving between 2000 and 2001 for the three breeding categories. The proportion of time spent diving was treated as the dependent variable, and breeding status and year were treated as fixed effects. Time of day was a covariate, and individual was treated as random effect nested within the year by breeding status interaction. We excluded dive samples conducted for actively nesting birds

because breeding murrelets spend significantly more time foraging during incubation and chick provisioning periods than during pre- and postbreeding periods (M.Z.P., unpublished data), and more birds bred in 2001.

Estimating Fecundity

We estimated fecundity (number of female young produced per female of breeding age) with two approaches. First, we calculated the product of the proportion of radiomarked birds of breeding age that bred, the rate of nest failure, and the sex ratio of female young (0.5, assuming an even sex ratio). Second, we estimated fecundity by conducting at-sea surveys from a small vessel along zig-zag transects from 200 to 2500 m from shore (Fig. 1) and calculating the juvenile ratio (Beissinger 1995; Becker et al. 1997). Surveys were conducted from 15 July to 22 August. Few juveniles are expected to fledge prior to 15 July, and after 22 August adults begin molting into basic plumage and resemble juveniles. To estimate fecundity from juvenile ratios, we corrected the ratio for the proportion of (1) juveniles that had not fledged when a survey was conducted and (2) after-hatch-year birds below age of first breeding. The first correction was done for each survey separately with the regression model of Beissinger (1995):

$$p = 0.012 * D - 1.919,$$

where p is the cumulative proportion of birds expected to fledge and D is the Julian date of the survey. For the second correction, we solved iteratively for the fecundity rate that produced the date-corrected juvenile ratio based on Beissinger's (1995) postbreeding, three-stage population model, assuming an adult survival rate of 0.85 and an age of first breeding of 3 years. We also used this procedure to estimate the proportion of birds below age of first breeding for fecundity derived from radiotelemetry.

Results

Proportion of Breeders

During the 2 years of study, 9 of the radiomarked murrelets nested (breeders), 12 did not nest but were in breeding condition (potential breeders), and 11 did not nest and were not in breeding condition (nonbreeders) (Table 3). Fourteen birds were not tracked long enough to determine whether they nested, and were considered of unknown breeding status. All five female breeders had elevated VTG levels, all but one had elevated levels of Ca, and all but one had a brood patch (Fig. 2). Of 10 females that did not initiate nesting, 6 had elevated levels of VTG or Ca and/or a brood patch and were classified as potential breeders. All four male breeders had brood patches; 6

Table 3. Proportion of Marbled Murrelets (\pm SE) that were breeders, potential breeders, and nonbreeders in 2000 ($n = 18$) and 2001 ($n = 14$).

Breeding status	2000	2001	Both years
Breeders	0.11 \pm 0.08	0.50 \pm 0.13	0.31 \pm 0.11
Potential breeders	0.44 \pm 0.12	0.29 \pm 0.12	0.37 \pm 0.12
Nonbreeders	0.44 \pm 0.12	0.21 \pm 0.11	0.33 \pm 0.12

of 13 males that did not nest had brood patches and were classified as potential breeders.

The proportion of birds in the three breeding categories (Table 3) differed significantly between years ($\chi^2 = 5.98$, $df = 2$, $p = 0.05$). For both years combined, only $31 \pm 11\%$ of the murrelets were breeders, $37 \pm 12\%$ were potential breeders, and $33 \pm 12\%$ were nonbreeders. When potential breeders and nonbreeders were pooled, the difference between years was due to a greater proportion of breeders in 2001 than in 2000 ($\chi^2 = 5.89$, $df = 1$, $p = 0.02$). In 2001, most birds either nested or were in breeding condition (breeders plus potential breeders, 0.79 ± 0.11). The proportion of birds with brood patches at the time of capture was greater in 2001 (0.77 ± 0.09) than in 2000 (0.54 ± 0.11). This difference was marginally significant ($\chi^2 = 2.70$, $df = 1$, $p = 0.10$). The proportion of females with elevated vitellogenin and calcium did not differ between the years ($\chi^2 = 0.01$, $df = 1$, $p = 0.94$, and $\chi^2 = 0.22$, $df = 1$, $p = 0.64$, respectively).

Rate and Causes of Nest Failure

We located seven nests, all of which failed. To increase our sample size, we report fates of all other nests found in the region (Appendix 1). Including those in this study, only 3 of 19 nests (0.16, SE = 0.08) successfully fledged young. Of 9 nests for which the cause of failure was determined conclusively, 6 (0.67, SE = 0.16) were depredated, including 4 (0.44, SE = 0.17) by corvids. Predation may

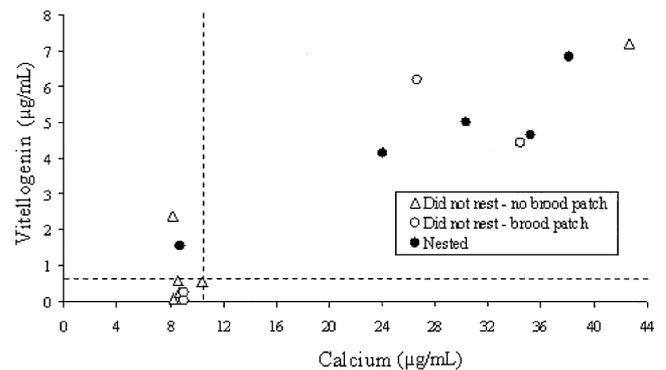


Figure 2. Plasma vitellogenin and calcium levels for 15 female Marbled Murrelets.

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

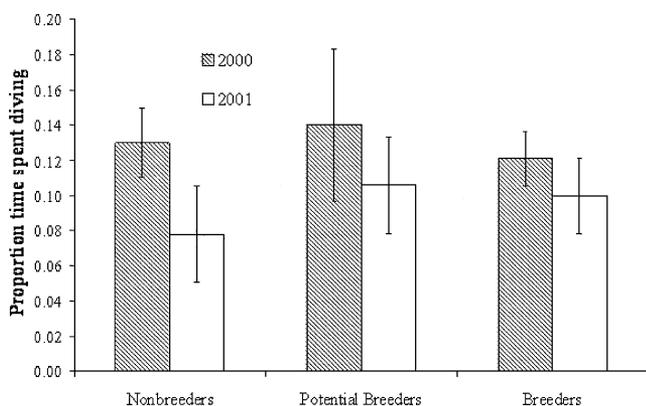


Figure 3. Mean proportion of time spent diving ($\pm 95\%$ confidence interval) by Marbled Murrelets of three different breeding categories in 2000 (hatched) and 2001 (white).

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 = 0.029) in 2001. The combined fecundity estimate for both years from at-sea surveys was 0.042 (SE = 0.023).

Discussion

The low fecundity estimate derived from at-sea surveys (0.042) was similar to the low fecundity estimate from radiotelemetry (0.027). Both estimates were well below levels needed to maintain the population (≥ 0.20 ; Beissinger 1995; Beissinger & Nur 1997). Thus, low reproductive success appears to limit Marbled Murrelet population growth in central California. A low proportion of breeders is partly responsible for poor reproduction. The proportion of breeders (0.31) was less than half the rate estimated for Marbled Murrelets in Desolation Sound, British Columbia (0.65), determined by similar methods (Bradley et al., 2004). Radio transmitters and remote recording devices can have negative effects on the behavior, energy budgets, and reproductive success of seabirds (Wilson et al. 1989; Culik & Wilson 1991; Croll et al. 1992; Watanuki et al. 1992). They could have disrupted the breeding of some murrelets and negatively biased the proportion of breeders. The proportion of breeders was much lower in this study than in British Columbia, however, where similar techniques were used, which strongly suggests that one or more environmental factors caused the difference between regions. In addition to a low proportion of breeders, a high rate of nest failure caused low reproductive success in this study. Nest success rate (0.16) was almost three times lower than in British Columbia (0.46; Bradley et al., 2004) and 40% lower than estimated for murrelets range-wide (0.28; Nelson & Hamer 1995b). Although more birds nested in 2001 than in 2000, nest failure was so high that few juveniles were produced.

Environmental Factors Limiting Murrelet Reproduction

Our predictions of the effects of food limitation on murrelet demography, behavior, and physiology were strongly upheld (Table 2). High levels of annual variation observed in these attributes supported an exclusive prediction of the food-limitation hypothesis. Not only did significantly more murrelets nest in 2001 than in 2000, but in 2001 a greater proportion of birds were in breeding condition with brood patches and the juvenile ratio was higher. Moreover, murrelets of all breeding categories spent significantly more time diving in 2000 than in 2001, indicating that birds had a harder time meeting their energetic requirements in 2000. Murrelets fly farther from nesting areas to forage under low food conditions (Becker & Becker 2003). Therefore, we suggest that low food availability limited the number of murrelets that nested in

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; Loughheed et al. 2002b; McFarlane-Tranquilla et al. 2003a), even though they did not initiate incubation (the relationship between brood patch and incubation status is unclear; McFarlane-Tranquilla et al. 2003a). Supplementary cues, such as the presence of a mate and a nest site, are believed to be required to stimulate ovary development (Farner & Gwinner 1980; Wingfield 1980), which occurs prior to elevation or development of the physiological indicators we used. If females with elevated vitellogenin or calcium had already selected a nest site at the time of capture and aborted breeding for other reasons, most radiomarked females located nests (Fig. 3) in 2000 (5 of 9, or 56%) and 2001 (4 of 6, or 67%). Nonbreeders, even though they were not in breeding condition, were unlikely to be limited by nest-site availability because they rarely flew inland to prospect for nests. More likely, nonbreeders were unable to achieve breeding condition (i.e., they were food-limited) or were too young to breed (two were known 1-year-old birds). Consequently, nest-site limita-

tion does not appear to be responsible for low reproduction of murrelets in central California. However, our analysis only examined factors currently limiting reproductive success and did not address the causes of the population decline from historic levels. Large-scale harvesting of old-growth forests since the late nineteenth century likely contributed to population declines in California (Carter & Erickson 1992). Further harvesting may reduce breeding population size (Burger 2001; Raphael et al. 2002) and increase nest predators favored by habitat fragmentation.

Diagnosing Causes of Population Declines

Among the six approaches identified in Table 1, testing multiple competing hypotheses (MCH) is the most universally applicable and has several advantages. First, it provides a unifying framework for simultaneously testing the effects of multiple potential limiting factors by combining several types of independent data. Second, the MCH approach does not necessarily require long-term data sets, information from multiple populations, or data taken prior to a decline. Nevertheless, to apply the MCH with rigor, at least some predicted effects of an attribute must differ among putative causes of decline. Unique predictions may not be possible for some attributes; for example, we could not discriminate among potential factors on the basis of nest failure rates or inland flight behavior alone (Table 2). Moreover, examining several different kinds of attributes and seeking concordance among predictions is necessary for rigorous inference. Ideally, all predictions for a particular factor would be supported by field tests, but simply because one or more predictions are not supported does not necessarily mean the factor is not limiting.

The best strategy for diagnosing causes of population declines is to employ several of the approaches in Table 1. This can be done within the context of the MCH by incorporating elements of each approach into the predictions. For example, one could predict that the proportion of breeders is greater for murrelet populations with more nesting habitat (i.e., the population-comparisons approach). We also suggest that combining mechanistic tests with analyses conducted over large spatial scales can provide considerable insight into causes of population declines. Experimental and MCH approaches identify mechanistically limiting factors, but they are often applied to one or a few populations. Insights gained from these two approaches can be extended by designing range-wide tests of limiting factors with the population-comparisons or timing-of-decline approaches or can be confirmed by the modeled-population-response approach.

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Literature Cited

- Becker, B. H. 2001. Effects of oceanographic variation on Marbled Murrelet diet and habitat selection. Ph.D. dissertation. University of California, Berkeley.
- Becker, B. H., and S. R. Beissinger. 2003. Scale-dependent habitat selection by a nearshore seabird, the Marbled Murrelet, in a highly dynamic upwelling system. *Marine Ecology Progress Series* **256**: 243-255.
- Becker, B. H., S. R. Beissinger, and H. R. Carter. 1997. At-sea density monitoring of Marbled Murrelets in central California: methodological considerations. *Condor* **99**:743-755.
- Beissinger, S. R. 1995. Population trends of the Marbled Murrelet projected from demographic analyses. Pages 385-393 in C. J. Ralph, G. L. Hunt Jr., M. G. Raphael, and J. F. Piatt, editors. Ecology and conservation of the Marbled Murrelet. General technical report PSW-GTR-152. U.S. Forest Service, Albany, California.
- Beissinger, S. R., and N. Nur. 1997. Population trends of the Marbled Murrelet projected from demographic analysis. Pages B1-B35 in Recovery plan for the Marbled Murrelet (*Brachyramphus marmoratus*) in Washington, Oregon, and California. U.S. Fish and Wildlife Service, Portland, Oregon.
- Böhning-Gaese, K., M. L. Taper, J. H. Brown. 1993. Are declines in North American insectivorous songbirds due to causes on the breeding range? *Conservation Biology* **7**:76-86.
- Bradley, R. W., F. Cooke, L. W. Loughheed, and W. S. Boyd. 2004. Inferring breeding success through radiotelemetry in the marbled murrelet. *Journal of Wildlife Management* **68**:in press.
- Burger, A. E. 2001. Using radar to estimate populations and assess habitat associations of Marbled Murrelets. *Journal of Wildlife Management* **65**:696-715.
- Burkett, E. B. 1995. Marbled Murrelet food habits and prey ecology. Pages 223-246 in C. J. Ralph, G. L. Hunt Jr., M. G. Raphael, and J. F. Piatt, editors. Ecology and conservation of the Marbled Murrelet. General technical report PSW-GTR-152. U.S. Forest Service, Albany, California.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.
- Cam, E., L. Loughheed, R. Bradley, and F. Cooke. 2003. Demographic assessment of a Marbled Murrelet population from capture-mark-recapture and radio-telemetry data. *Conservation Biology* **17**:1118-1126.
- Carter, H. R., and R. A. Erickson. 1992. Status and conservation of the Marbled Murrelet in California. *Proceedings of the Western Foundation of Vertebrate Zoology* **5**:92-116.
- Caughley, G. 1994. Directions in conservation biology. *Journal of Animal Ecology* **62**:215-244.
- Caughley, G., and A. Gunn. 1996. Conservation biology in theory and practice. Blackwell Sciences, Cambridge, Massachusetts.
- Cooper, C. B., and J. R. Walters. 2002. Experimental evidence of disrupted dispersal causing decline of an Australian passerine in fragmented habitat. *Conservation Biology* **16**:471-478.
- Croll, D. A., A. J. Gaston, A. E. Burger, and D. Konnoff. 1992. Foraging behavior and physiological adaptation for diving in thick-billed murre. *Ecology* **73**:344-356.
- Culik, B. M., and R. P. Wilson. 1991. Energetics of underwater swimming in Adelie Penguins (*Pygoscelis adellie*). *Journal of Comparative Physiology* **161**:285-291.
- Davies, K. F., C. R. Margules, and K. F. Lawrence. 2000. Which species traits predict population declines in experimental forest fragments? *Ecology* **81**:1450-1461.
- Farner, D. S., and E. Gwynner. 1980. Photoperiodicity, circannual and reproductive cycles and reproductive cycles. Pages 331-366 in A. Epple and M. H. Stetson, editors. *Avian Endocrinology*. Academic Press, New York.
- Green, R. E. 1995. Diagnosing causes of bird population declines. *Ibis* **137**:S47-S55.
- Green, R. E. 2002. Diagnosing causes of population declines and selecting remedial actions. Pages 139-156 in K. Norris and D. J. Pain, editors. *Conserving bird biodiversity: general principles and their application*. Conservation biology series 7. Cambridge University Press, Cambridge, United Kingdom.
- Green, R. E., and G. J. M. Hiron. 1991. The relevance of population studies to the conservation of threatened birds. Pages 594-633 in C. M. Perrins, J. D. Lebreton, and G. J. M. Hiron, editors. *Bird population studies*. Oxford University Press, Oxford, United Kingdom.
- Hamer, T. E., and S. K. Nelson. 1995. Nesting chronology of the Marbled Murrelets. Pages 49-56 in C. J. Ralph, G. L. Hunt Jr., M. G. Raphael, and J. F. Piatt, editors. Ecology and conservation of the Marbled Murrelet. General technical report PSW-GTR-152. U.S. Forest Service, Albany, California.
- Ivins, G. K., G. D. Weddle, and W. H. Halliwell. 1978. Hematology and serum chemistries in birds of prey. Page 386 in M. B. Fowler, editor. *Zoo and wild animal medicine*. W. B. Saunders, Philadelphia.
- Jodice, P. G., and M. W. Collopy. 1999. Diving and foraging patterns of Marbled Murrelets (*Brachyramphus marmoratus*): testing predictions from optimal-breathing patterns. *Canadian Journal of Zoology* **77**:1419-1418.
- Kenward, R. 1987. Wildlife radio tagging: equipment, field techniques and data analysis. Academic Press, London.
- Liebezeit, J. R., and T. L. George. 2002. A summary of predation by Corvids on threatened and endangered species in California and management recommendations to reduce Corvid predation. Species conservation and recovery program report 2002-02. California Department of Fish and Game, Sacramento.
- Lips, K. R. 1998. Decline of a tropical montane amphibian fauna. *Conservation Biology* **12**:106-117.
- Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS system for mixed models. SAS Institute, Cary, North Carolina.
- Loughheed, C., L. W. Loughheed, F. Cooke, and S. Boyd. 2002a. Local survival of adult and juvenile Marbled Murrelets and their importance for estimating reproductive success. *Condor* **104**:309-318.
- Loughheed, C., B. A. Vanderkist, L. W. Loughheed, and F. Cooke. 2002b. Techniques for investigating breeding chronology in Marbled Murrelets and their importance for estimating reproductive success. *Condor* **104**:319-329.
- McCulloch, N., and K. Norris. 2001. Diagnosing the cause of population changes: localized habitat change and the decline of the endangered St. Helena Wirebird. *Journal of Applied Ecology* **38**:771-783.
- McFarlane-Tranquilla, L., T. D. Williams, and F. Cooke. 2003a. Using vitellogenin to examine interannual variation in breeding chronology of Marbled Murrelets (*Brachyramphus marmoratus*). *Auk* **120**: 512-521.
- McFarlane-Tranquilla, L. A., R. W. Bradley, D. Lank, T. G. Williams, L. W. Loughheed, and F. Cooke. 2003b. The reliability of brood patches in assessing reproductive status in the Marbled Murrelet: words of caution. *Waterbirds* **26**:108-118.
- Mitchell, M. A., and A. J. Carlisle. 1991. Plasma zinc as an index of vitellogenin production and reproductive status in the domestic fowl. *Comparative Biochemistry and Physiology* **100A**:719-724.
- Nelson, S. K. 1997. Marbled Murrelet. Pages 1-25 in A. Poole, P. Stettenheim, and A. Gill, editors. *Birds of North America*. Academy of

- Natural Sciences of Philadelphia and the American Ornithologists' Union, Washington, D.C.
- Nelson, S. K., and T. E. Hamer. 1995a. Nesting biology and behavior of the Marbled Murrelet. Pages 57-67 in C. J. Ralph, G. L. Hunt Jr., M. G. Raphael, and J. F. Piatt, editors. Ecology and conservation of the Marbled Murrelet. General technical report PSW-GTR-152. U.S. Forest Service, Albany, California.
- Nelson, S. K., and T. E. Hamer. 1995b. Nest success and effects of predation on Marbled Murrelets. Pages 89-97 in C. J. Ralph, G. L. Hunt Jr., M. G. Raphael, and J. F. Piatt, editors. Ecology and conservation of the Marbled Murrelet. General technical report PSW-GTR-152. U.S. Forest Service, Albany, California.
- Newman, S. H., J. F. Piatt, and J. White. 1997. Hematological and plasma biochemical reference ranges of Alaskan seabirds: their ecological significance and clinical importance. *Colonial Waterbirds* **20**: 492-514.
- Newman, S. H., J. Y. Takekawa, D. L. Whitworth, and E. Burkett. 1999. Subcutaneous anchor attachment increases retention of radio-transmitters on Xantus' and Marbled Murrelets. *Journal of Field Ornithology* **70**:520-534.
- Pascual, M. A., and M. Adkison. 1994. The decline of the Steller Sea Lion in the northeast Pacific: demography, harvest or environment. *Ecological Applications* **4**:393-403.
- Peery, M. Z., S. R. Beissinger, S. H. Newman, B. H. Becker, E. Burkett, and T. D. Williams. 2004. Individual and temporal variation in inland flight behavior of marbled murrelets: implications for population monitoring. *Condor* **106**:344-353.
- Platt, J. R. 1964. Strong inference. *Science* **146**:347-353.
- Popper, K. R. 1959. The logic science of scientific discovery. Basic Books, New York.
- Raphael, M. G., D. E. Mack, and B. Cooper. 2002. Landscape-scale relations between abundance of Marbled Murrelets and distribution of nesting habitat. *Condor* **104**:331-342.
- Savidge, J. A. 1987. Extinction of an island forest avifauna by an introduced snake. *Ecology* **68**:660-668.
- Sealy, S. G. 1972. Adaptive differences in breeding biology in the marine bird family Alcidae. Ph.D. dissertation. University of Michigan, Ann Arbor.
- Singer, S. W., N. L. Naslund, S. A. Singer, and C. J. Ralph. 1991. Discovery and observation of two nest trees of the Marbled Murrelet. *Condor* **93**:330-339.
- Singer, S. W., D. L. Suddjian, and S. A. Singer. 1995. Fledging behavior, flight patterns, and forest characteristics at Marbled Murrelet tree nests in California. *Northwestern Naturalist* **76**:54-62.
- Stallard, R. F. 2001. Possible environmental factors underlying amphibian decline in Eastern Puerto Rico: analysis of U.S. government data archives. *Conservation Biology* **15**:943-953.
- U.S. Fish and Wildlife Service (USFWS). 1997. Recovery plan for the Marbled Murrelet (*Brachyramphus marmoratus*) in Washington, Oregon, and California. USFWS, Portland, Oregon.
- Vanderkist, B. A., X. Xue, R. Griffiths, K. Martin, W. Beauchamp, and T. D. Williams. 1999. Evidence of male-bias in capture samples of Marbled Murrelets from genetic studies in British Columbia. *Condor* **101**:398-402.
- Vanderkist, B. A., T. D. Williams, D. F. Bertram, L. Lougheed, and J. P. Ryder. 2000. Indirect, physiological indicators of reproduction in the Marbled Murrelet. *Functional Ecology* **14**:758-765.
- Wanless, S., J. A. Morris, and M. P. Harris. 1988. Diving behavior of the guillemot *Uria aalge*, puffin *Fratrercula articularia*, and razorbill *Alca torda* as shown by radio-telemetry. *Journal of Zoology, London* **216**:73-81.
- Watanuki, Y., Y. Mori, and Y. Naito. 1992. Adelie Penguins parental activities and reproduction: effects of device size and timing of its attachment during chick-rearing period. *Polar Biology* **12**:539-544.
- Whitworth, D. L., J. Y. Takekawa, H. R. Carter, and W. R. McIver. 1997. Night-lighting as an at-sea capture technique for Xantus' Murrelets in the Southern California Bight. *Colonial Waterbirds* **20**:525-531.
- Wilson, R. P., N. R. Coria, H. J. Spairani, D. Adelung, and B. Culik. 1989. Human induced behavior in Adelie Penguins *Pygoscelis adeliae*. *Polar Biology* **10**:77-80.
- Wingfield, J. C. 1980. Fine temporal adjustment of reproductive functions. Pages 367-389 in A. Epple, M. H. Stetson, editors. Avian endocrinology. Academic Press, New York.
- Yates, C. J., and L. M. Broadhurst. 2002. Assessing limitations on population growth in two critically endangered *Acacia* taxa. *Biological Conservation* **108**:13-16.

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

Nest site name	Easting UTM	Northing UTM	Year	Fate	Failure		Source
					stage ^a	cause ^b	
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	569737	4113368	2001	failed	I	unknown, possible predation	this study
Campground #1							
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	569480	4113390	2002	failed	N	predated by CORA	D. Suddjian, unpublished data
Campground #2							
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

^aI, incubation; N, nestling; U, unknown.

^bCORA, Common Raven (*Corvus corax*); STJA, Steller's Jay (*Cyanocitta stelleri*); RSHA, Red-shouldered Hawk (*Buteo lineatus*); UTM, universal transverse mercator.

^cAdult predated at nest site.

