

**STELLER'S JAY CONDITIONED TASTE AVERSION TREATMENT
IN THE SANTA CRUZ MOUNTAINS IN 2012**

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Steller's Jay Conditioned Taste Aversion Treatment In the Santa Cruz Mountains In 2012

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Introduction

Predation on eggs of marbled murrelets (*Brachyramphus marmoratus*) has been linked to poor recruitment of young into the murrelet population, especially in the California, Oregon and Washington populations (McShane et al. 2004, Hébert and Golightly 2007, Golightly and Schneider 2009, Peery and Henry 2010). Corvids have been implicated as the most influential egg predators on murrelets. Fragmented forests provide the only remaining murrelet nesting habitat in California; unfortunately, these forests also support great densities of opportunistic corvids like Steller's jays (*Cyanocitta stelleri*). These same forests are also popular destinations for recreating humans who may add to corvid densities by adding nutritional resources. This increases predation risk on murrelet eggs (Marzluff et al. 2004, Marzluff and Neatherlin 2006, Golightly and Gabriel 2009, Malt and Lank 2009). Effective reductions of egg predation require manipulation of the predator population density or predation behavior.

Conditioned taste aversion (CTA) techniques for Steller's jays that exposed the jays to murrelet-colored and sized eggs treated with carbachol (carbamylcholine chloride) effectively induced subsequent aversion to the murrelet-mimic eggs (Gabriel and Golightly 2011). In laboratory tests, aversion conditioning increased attack latencies on murrelet-mimic eggs compared to control eggs between the initial and repeat exposures, and the strength of aversions remained constant over time.

In Redwood National Park, CTA treatment reduced corvid predation on murrelet-mimic eggs by 37% to 72% in comparison to control eggs (Gabriel and Golightly 2011). Attack rates on murrelet-mimic eggs were already 12% less than attack rates on control eggs during the initial deployment, suggesting that the density of egg deployment used in Redwood National Park (1 murrelet mimic egg / 2 ha; Gabriel and Golightly 2011) resulted in many jays encountering more than one treated murrelet-mimic eggs within their territories. Thus that study probably underestimated the potential for conditioned taste aversion, and treatment is expected to be effective at considerably lower egg densities. Peery and Henry (2010) calculated that reductions in corvid predation on murrelet nests between 40 and 70% (depending on a range of assumptions

regarding nesting ratios and predation rates) would be necessary to stabilize the imperiled marbled murrelet population segment located in central California. To improve reproductive success of murrelets in central California, CTA was used as a management technique in Butano State Park and Portola Redwoods State Park in spring 2012.

Methods

The distribution of habitat important to murrelet recovery and currently occupied by murrelets in central California was identified by the U.S. Fish and Wildlife Service (USFWS 2008). CTA treatment was focused on 600 ha of forested areas surrounding high-visitor use areas of Butano State Park and Portola Redwoods State Park in San Mateo County in spring 2012. Treatment consisted of deployment of carbachol-laced eggs that mimicked murrelet eggs in contiguous habitat used by jays in old growth or second growth forest stands around campgrounds. Deployment areas were based on reports that anthropogenic habitat alteration and food supplementation affected jay populations within 1 to 2 km of high-use visitor attractions (W. Goldenberg, L. George, J. Black, and E. Doucet-Ber, Z. Peery, unpublished data). Furthermore, the forest surrounding the parks and campgrounds that were the focus of treatment was very fragmented, and thus very attractive to populations of Steller's jays. We used the rationale that, instead of merely treating islands of murrelet breeding habitat, edges between murrelet breeding habitat and surrounding forest were particularly important for treating jays that may be predated murrelet nests (Marzluff et al. 2004, Malt and Lank 2009).

Egg preparation

Laboratory preparation of treatment eggs began in February using raw, small-sized chicken eggs that weighed 42 to 45 g. A small hole of approximately 3 mm diameter was drilled in the narrowest end of the shell using a rotary tool. We extracted 0.5 to 1 ml of egg contents with a syringe to provide for the subsequent addition of aversive chemical solution and for expansion of egg contents with temperature. We then injected at least 0.24 ml of a solution containing 100 mg carbachol (carbamylcholine chloride, 99%, Acros Organics, Thermo Fisher Scientific, New Jersey, U.S.A) per 1 ml sterile water (24 mg carbachol / egg). A piece of wire approximately 2 mm in diameter, with the tip bent at an approximate angle of 10° and attached to a rotary tool was inserted into the drilled hole. The rotary tool was activated for 1 to 2 s, resulting in a short burst of whisking to thoroughly blend the contents of the egg with the carbachol solution. The

egg surface was then wiped clean and the hole sealed with hot glue (Dualmelt G GS25DT, Stanley Tools, Connecticut, U.S.A.).

Eggs were colored with paint in a blue-green hue closely resembling murrelet eggs (Oceanfront 660, Benjamin Moore & Co., New Jersey, U.S.A.) using an airbrush. Irregular black spotting as displayed on murrelet eggs was applied with dilute acrylic paint. A 20 cm black zip tie (8" x 3/16" Black Nylon Cable Tie; Storehouse, Harbor Freight Tools, Camarillo, California, U.S.A.) was then attached with hot glue to all eggs along 2 cm of their widest side. Initially, many eggs detached easily from the hot glued zip tie. Subsequently (from 15 March forward) the attachment method was modified by attaching an approximately 1 cm² piece of double sided hook-and-loop fastener (Velcro brand) with hot-glue to both the egg and the zip tie. This modification provided flexibility to the egg-zip tie joint.

Field deployment

Two temporally distinct deployments of treatment eggs were implemented. Jay territories largely overlap among mates and to varying degrees among neighbors (Brown 1963), and predation by rodents may have caused some loss of treatment eggs. Consequently, some jays may not have been exposed to eggs in the first deployment. The goal of a second deployment was to maximize the number of jays exposed to treatment eggs. The first field deployment was conducted between 23 February and 15 May, and the second treatment between 19 March and 5 June. Removal of egg remains and egg-attachment materials occurred between 2 May and 19 July.

Treatment eggs were placed at intervals of 100 m along roads and trails throughout the parks in the areas surrounding high-use visitor attractions. Eggs were placed in trees that provided a branch suitable for placing an egg in the sub-canopy, between 3 and 4 m height above ground. Given the great density of trails surrounding high-visitor use areas in the central California parks, treatment density approximated between 0.5 to 2 treatment eggs / ha. The use of roads and trails for egg deployment resulted in the greatest treatment densities in areas with greatest density of human development, and coincided with greatest expected jay densities (Bensen 2008, Suddjian 2009). In the first deployment, 431 treated eggs were placed in Butano State Park (Fig. 1), and 134 treated eggs were placed in Portola Redwoods State Park (Fig. 2).

During the second deployment of treated eggs, the disposition of eggs placed during the first deployment was determined. This resulted in intervals of 14 to 65 days between the first deployment and assessment of egg predation. During the removal of remains after the second

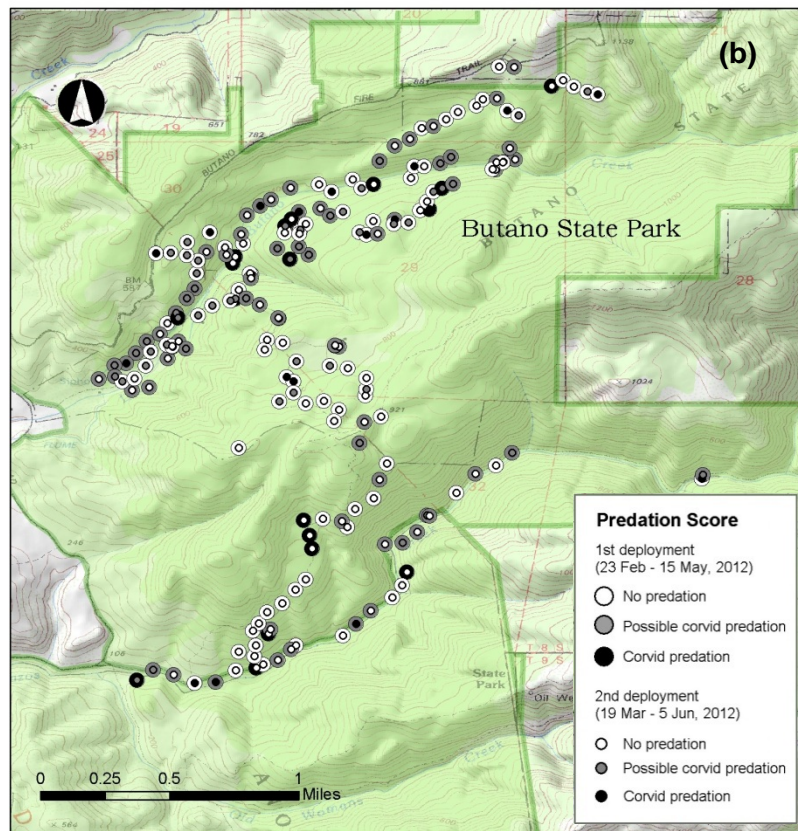
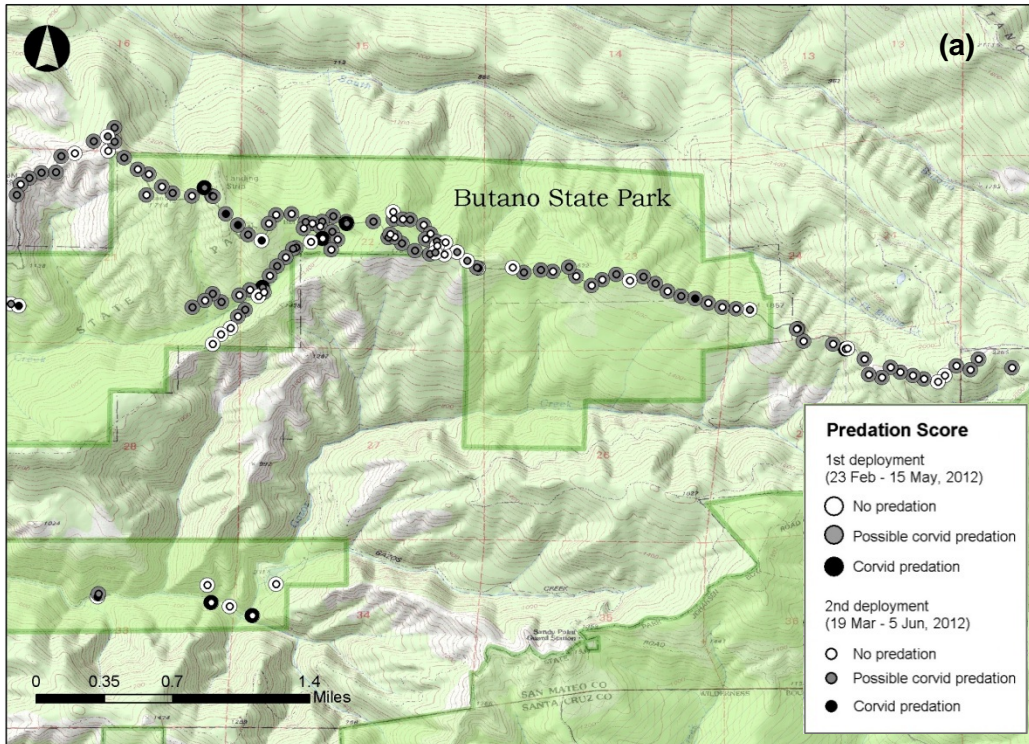


Figure 1. Deployment areas and indices of predation (see Table 1) of murrelet-mimic eggs from 2 consecutive deployments in the eastern (a) and western (b) areas of Butano State Park, California.

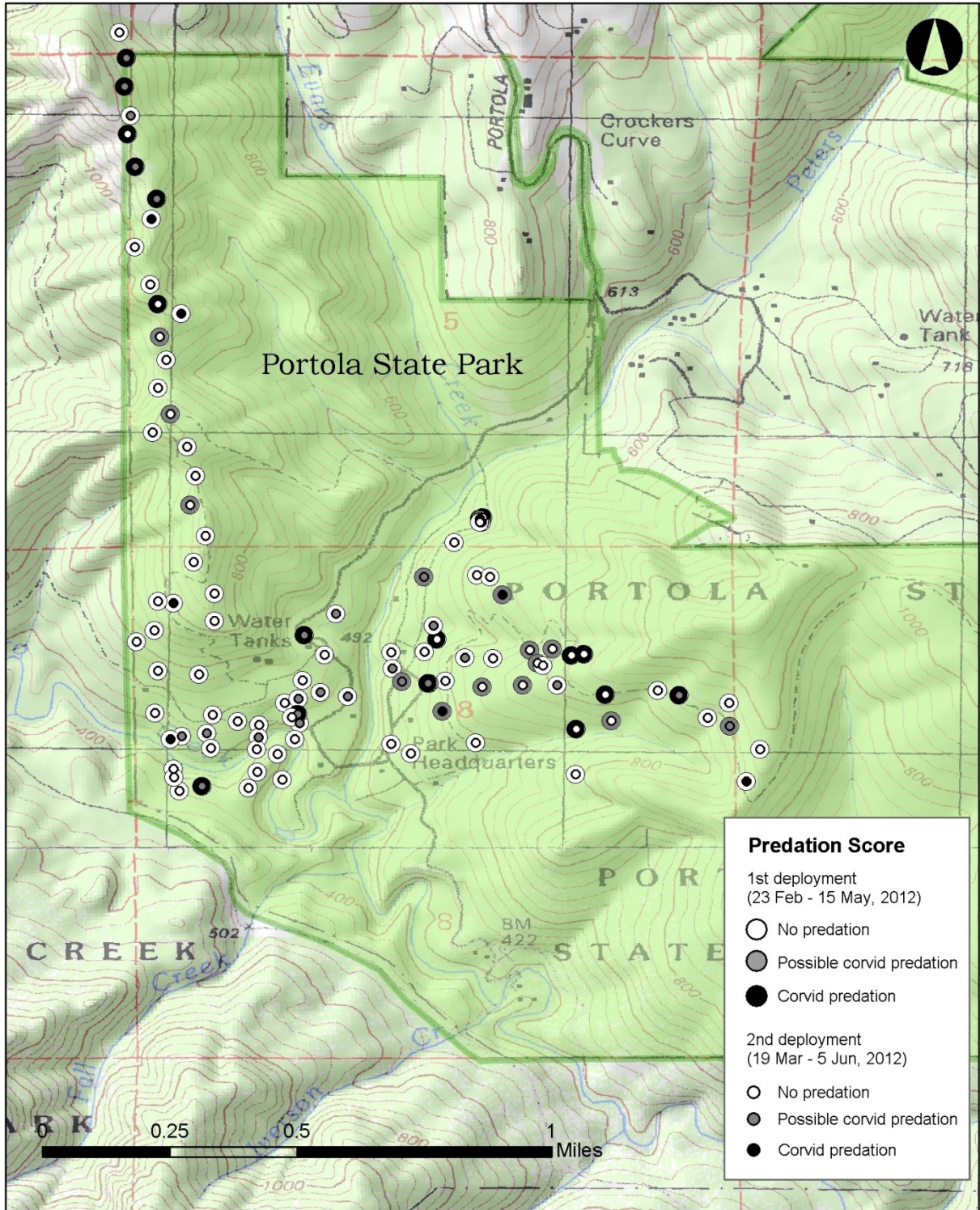


Figure 2. Deployment area and indices of predation (see Table 1) of murrelet-mimic eggs from 2 consecutive deployments in Portola Redwoods State Park, California.

deployment, the disposition of eggs placed during the second deployment was determined. This resulted in intervals of 6 to 82 days between the second deployment and assessment of egg predation. Disposition of eggs was scored in three categories based on the likelihood that they had been predated (Table 1).

Table 1. Predation categories assigned to eggs after first and second deployment of carbachol-treated murrelet-mimic eggs in central California parks for aversive conditioning of wild Steller’s Jays.

Predation category	Description of egg disposition
No predation	Egg was intact
Possible corvid predation	Egg showed sign of unknown predator, or egg missing
Corvid predation	Egg remains showed conclusive signs of corvid attack
Unknown	Eggs or egg remains were found, but not enough evidence collected to assign predation category ^a

^aIntact eggs (no predation) could almost always, and missing eggs (possible corvid predation) could always be unambiguously assigned; thus proportions of assigned predation classes overrepresent the category ‘no predation’, probably underrepresent the category ‘possible corvid predation’, and most strongly underrepresent the category ‘corvid predation’.

The effectiveness of CTA and adequacy of the density of deployed eggs in protecting murrelet-mimic eggs from predation was determined by comparing the predation rate of murrelet-mimic eggs between the first and second egg deployments. First we compared the overall proportions of predated mimic eggs in the two deployments. Second we compared the proportions of predation on mimic eggs located in or close to campgrounds within the treatment area to the remainder of the treatment area. We used Chi-square tests to compare proportions of mimic eggs in each predation category (not predated, possibly corvid predated, and corvid predated). When significant differences in these proportions between the respective sets of eggs (first deployment compared to second deployment, or within campgrounds compared to outside campgrounds, or close to campgrounds compared to away from campgrounds) were found, we then used two different groupings of predation categories for more detailed comparisons; for a maximally inclusive measure of corvid predation, eggs that were categorized as possibly corvid predated and as corvid predated were added together and compared to eggs that were not predated; for a maximally stringent measure of corvid predation only eggs that were categorized as corvid predated were used and contrasted to eggs that were not predated, whereas eggs categorized as possibly corvid predated were excluded from comparisons. Where contingency tables contained expected counts below 5 in any category, we used Fisher’s exact test (for 2x2 tables) or Monte Carlo simulations with 10,000 iterations to estimate Chi-Square and P-values (for larger tables).

We examined whether proportions of predation scores differed between the first deployment and the second deployment. We included only locations that had been revisited 14 to 35 days after deployment, or if the egg was found intact (not predated) any time after 14 days; these criteria were comparable to the time interval that was found to be suitable for correct classification of predation in the field assessment of CTA effectiveness on jays in Redwood National Park (Gabriel & Golightly 2011). Note that under this set of criteria, unpredated eggs were overrepresented relative to a direct count of eggs scored for each predation category. The imbalance among predation categories influenced interpretation of the absolute distribution of predation scores, but not the relative change between the first and second deployments.

Utilization of data collected only within 14 to 35 days after each deployment resulted in inadequate sample sizes to allow separate analysis of the two parks, and for any spatial analyses. We therefore repeated the examination whether proportions of predation scores differed between the first deployment and the second deployment under less rigorous criteria where all egg locations were included that could be classified as not predated, possibly corvid predated, or corvid predated (see Table 1). This second set of analyses allowed examination of predation patterns separately for Butano State Park and Portola Redwoods State Park, as well as a direct comparison of changes in overall predation between the first and second deployment with spatial distributions of predation in and outside of campgrounds. Under these criteria, unpredated eggs were also overrepresented relative to the other two predation categories (for details see Table 1), but not as strongly as under the first set of criteria described in the preceding paragraph.

We assessed whether effectiveness of CTA treatment and adequacy of deployment density differed between campgrounds and areas outside of campgrounds. For this purpose we compared proportions of predation scores between egg locations in campgrounds to locations outside campgrounds (Fig. 3) in the first deployment and again in the second deployment. Using an estimated 1 km radius of anthropogenic effects of campgrounds on jay populations (W. Goldenberg, L. George, and J. Black, unpublished data), we also compared proportions of predation scores between egg locations within 1 km of campgrounds to egg locations more than 1 km away from campgrounds (Fig. 3). Because of sample size limitations, no selection criteria regarding revisitation intervals were applied to the data for these analyses; instead all egg locations were included that could be assigned with a disposition score (not predated, possibly corvid predated, or corvid predated; see Table 1).

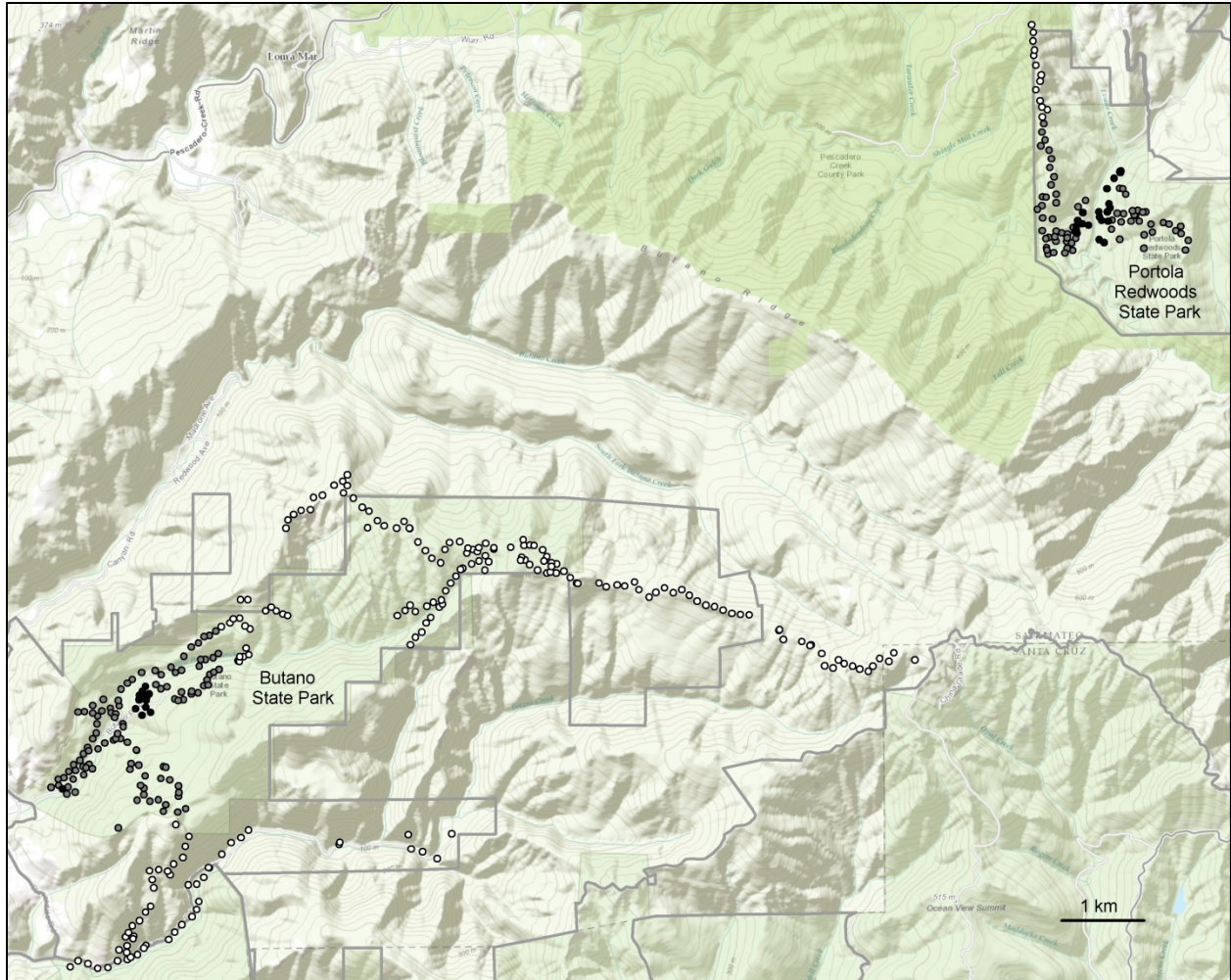


Figure 3. Deployment locations of murrelet-mimic eggs in campgrounds (black circles), within 1km of campgrounds (gray circles), and more than 1 km away from campgrounds (white circles) in Butano State Park and Portola Redwoods State Park, California.

We also monitored interactions of corvids and other species with treated eggs with infra-red motion sensor cameras (Trophy Cam Trail Camera, Bushnell Outdoor Products, Kansas, U.S.A.).

Cameras were placed at egg locations distributed throughout the deployment area and visited approximately once a week. Five cameras were placed at 5 different egg locations in Portola Redwoods State Park. Five other cameras were placed along Jackson Flat Trail in Butano State Park. On 2 May, the latter five cameras were moved to the Butano campground to improve chances of capturing images of jays interacting with eggs. Once a camera-monitored egg was predated, the egg was replaced. If predation by a non-corvid predator was suspected, the immediate surroundings of the tree were searched for any animals or sign of animals. Photos

obtained from trail cameras allowed identification of predators and behavioral evaluation of animal interactions with treated eggs.

Results

In the first egg deployment, 49% of revisited egg locations were not predated, while 10% of locations could not be assigned with a predation score. In the second field deployment, 55% of revisited egg locations were not predated, while 7% of locations could not be assigned with a predation score (Table 2). Eggs that could not be assigned with a predation score were excluded from further analyses.

Table 2. Disposition of eggs after first (1st) and second egg deployments (2nd) of murrelet-mimic eggs in Butano State Park and Portola Redwoods State Park. Number of eggs shown when including predation categories for all eggs assigned according to Table 1 (all), and when including only eggs revisited 14 to 35 days after deployment or, if the egg was found intact any time after 14 days (14-35 d).

Predation outcome	Criteria: all		Criteria: 14-35 d	
	1 st	2 nd	1 st	2 nd
<i>Butano State Park</i>				
Predated by corvid	28	18	11	4
Possibly predated by corvid	157	110	20	28
Not predated	177	196	177	181
<i>Portola Redwoods State Park</i>				
Predated by corvid	10	6	9	0
Possibly predated by corvid	21	32	20	0
Not predated	79	87	79	87
<i>Total for both parks combined</i>				
Predated by corvid	38	24	20	4
Possibly predated by corvid	178	142	40	28
Not predated	256	283	256	268
<i>Total eggs with valid predation score</i>	472	449	316	300
<i>Total eggs excluded by criteria</i>	55	35	211	184
<i>Total eggs revisited</i>	527	484	527	484

Trail cameras acquired 432 pictures of six different wildlife species interacting with or moving in close vicinity of mimic eggs. Series of photographs that were acquired within 10 minutes of each other at the same location likely depicted the same individual animal and were interpreted cumulatively as single interactions. According to these criteria, we identified 51 unique wildlife interactions. Note that many interactions involved the same species at the same location or several nearby locations that may have been in close enough proximity to be included in the same home range. The 51 unique interactions may therefore have included multiple recorded interactions of the same individual animals. Forty-five (88%) of these interactions were Steller's jays (Figs. 4, 5). No pictures occurred of jays eating egg contents, but in two photo series jays appeared to be separating the egg from the Velcro attachment (see Fig. 4). We acquired two interactions of western gray squirrels (*Sciurus griseus*; Fig. 6a, b), one unknown owl (Fig. 6b, c), one gray fox (*Urocyon cinereoargenteus*; Fig. 6 d, e), and one American robin (*Turdus migratorius*). We also had one photograph of the tail of an unknown mammal.



Figure 4. Series of photographs taken by a trail camera in central California parks showing a juvenile Steller's jay interacting with a carbachol-laced murrelet-mimic egg.



Figure 5. Photographs taken by trail cameras in central California parks showing Steller's jays interacting with carbachol-laced murrelet-mimic eggs.

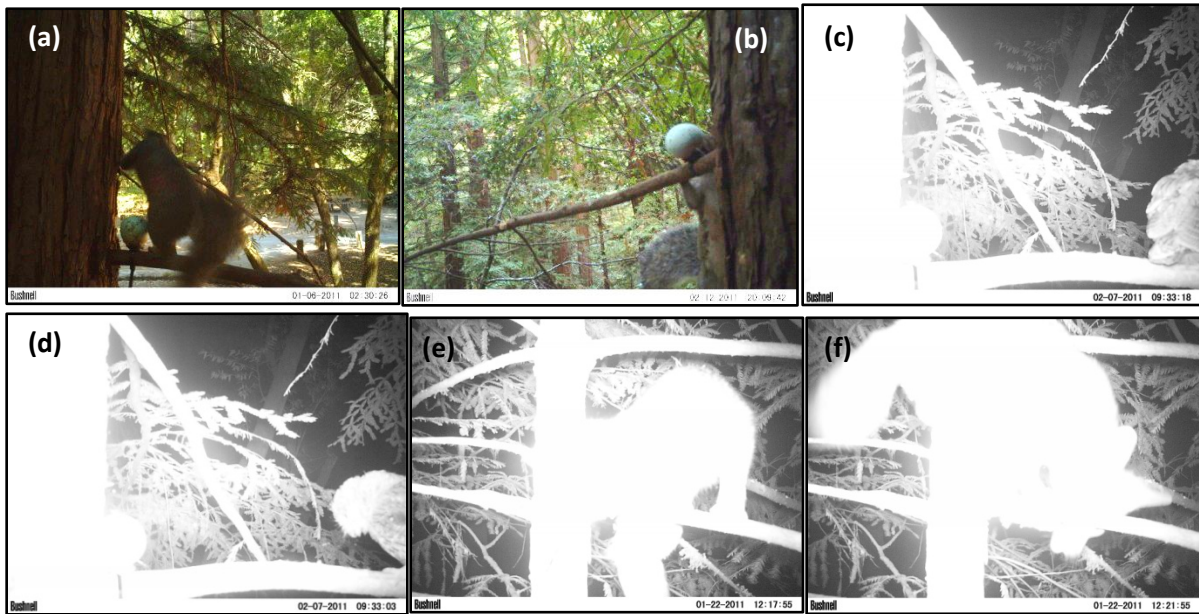


Figure 6. Photographs taken by trail cameras in central California parks showing two interactions by squirrels (a, b), one owl (c, d) and one grey fox (e, f) interacting with carbachol-laced murrelet-mimic eggs.

CTA effects including only eggs revisited after 14 to 35 days

Combining egg locations for both parks, the distribution of predation scores differed between the first and second deployments ($X^2_2 = 12.65$, $P < 0.001$, Fig. 7). Using maximally inclusive measures (possibly corvid predated and corvid predated eggs combined, see Fig. 7), the proportion of murrelet-mimic eggs predated in the second deployment was 44% less than in the first deployment ($X^2_1 = 8.387$, $P = 0.004$). Using maximally stringent measures (only corvid predated eggs included, see Fig. 7), the proportion of murrelet-mimic eggs predated in the second deployment was 80% less than in the first deployment ($X^2_1 = 10.913$, $P < 0.001$).

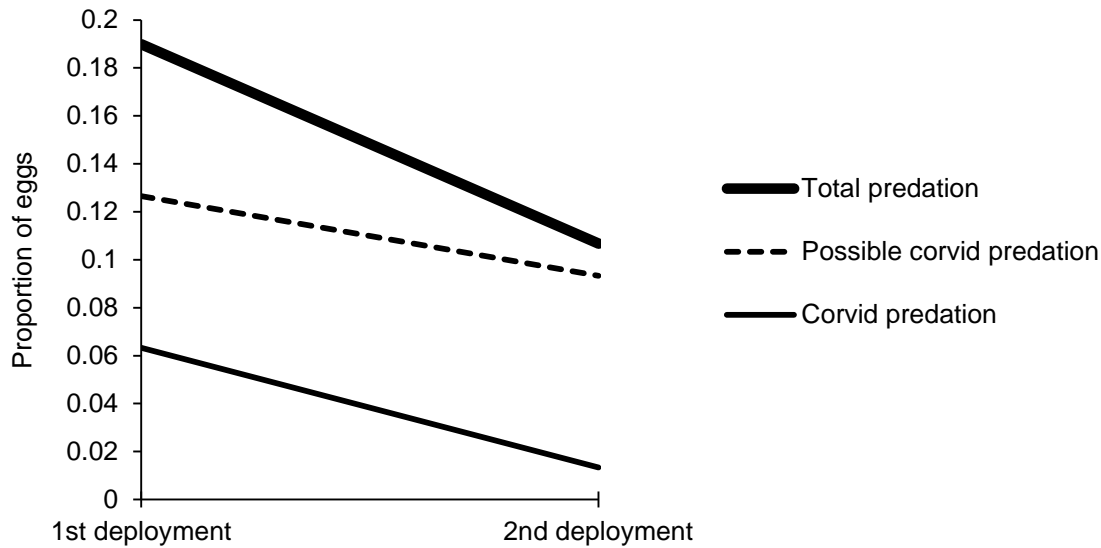


Figure 7. Proportion of eggs in three disposition categories, excluding unknown disposition, and assessed within 14 to 35 days after deployments, or if unpredated any time after 14 days, after first ($n = 316$) and second deployments ($n = 300$) of murrelet-mimic eggs in Butano State Park and Portola Redwoods State Park. Predation categories are described in Table 1.

CTA effects including all eggs with assigned predation scores

In Butano State Park, the distribution of predation scores differed between the first and second deployments ($X^2_2 = 9.34$, $P = 0.009$; Fig. 8). Using maximally inclusive measures, the proportion of murrelet-mimic eggs predated in the second deployment was 23% less than in the first deployment ($X^2_1 = 9.272$, $P = 0.002$; Fig. 8). Using maximally stringent measures, the proportion of murrelet-mimic eggs predated in the second deployment was 38% less than in the first deployment, but the difference was not significant ($X^2_1 = 5.95$, $P = 0.086$, Fig. 8). In Portola

Redwoods State Park, the distribution of predation scores did not differ between the first and second deployments ($X^2_2 = 2.72$, $P = 0.256$; Fig. 8).

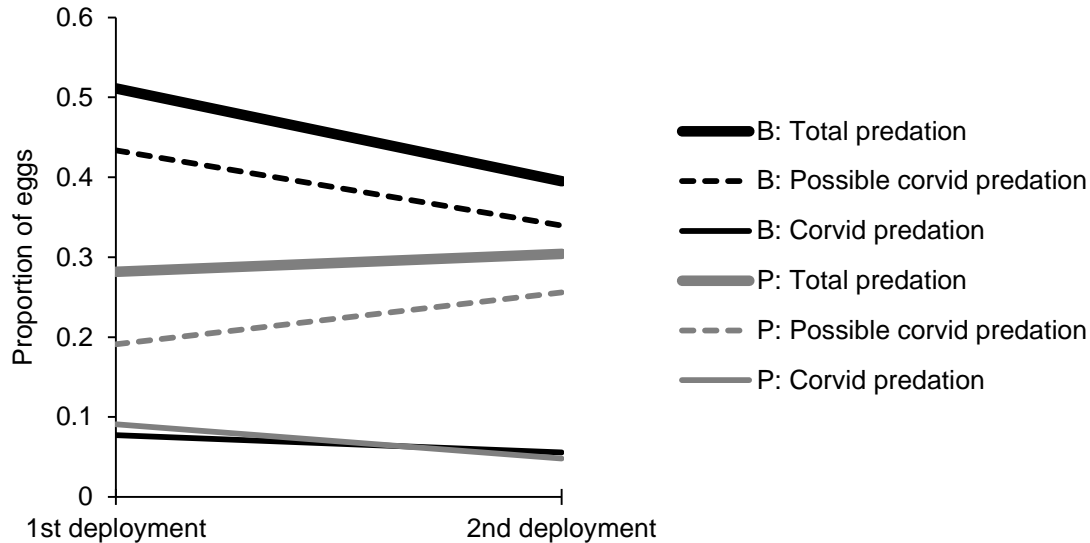


Figure 8. Proportion of eggs in three disposition categories, excluding unknown disposition, after first and second deployments of murrelet-mimic eggs in Butano State Park (B; $n_{1st} = 362$, $n_{2nd} = 324$) and Portola Redwoods State Park (P; $n_{1st} = 110$, $n_{2nd} = 125$). Predation categories are described in Table 1.

Combining egg locations for both parks, the distribution of predation scores differed between the first and second deployments ($X^2_2 = 7.994$, $P = 0.018$). Using maximally inclusive measures, the proportion of murrelet-mimic eggs predated in the second deployment was 19% less than in the first deployment ($X^2_1 = 7.327$, $P = 0.007$). Using maximally stringent measures, the proportion of murrelet-mimic eggs predated in the second deployment was 40% less than in the first deployment ($X^2_1 = 4.235$, $P = 0.040$).

Comparisons between egg locations relative to campgrounds

In the first deployment, the distribution of predation scores did not differ between egg locations in campgrounds and locations outside of campgrounds ($X^2_2 = 3.354$, $P = 0.187$, Fig. 9). In the second deployment, the distribution of predation scores differed between egg locations in campgrounds and locations outside of campgrounds ($X^2_2 = 6.037$, $P = 0.044$, Fig. 9). Using maximally inclusive measures (possibly corvid predated and corvid predated eggs combined, see Fig. 9), the proportion of murrelet-mimic eggs predated in campgrounds was 43% greater than

outside of campgrounds, although the difference was not significant (Fisher’s exact test, $P = 0.059$). Using maximally stringent measures (only corvid predated eggs included, see Fig. 9) the proportion of predated murrelet-mimic eggs did not differ between locations in and outside of campgrounds (Fisher’s exact test, $P = 0.999$).

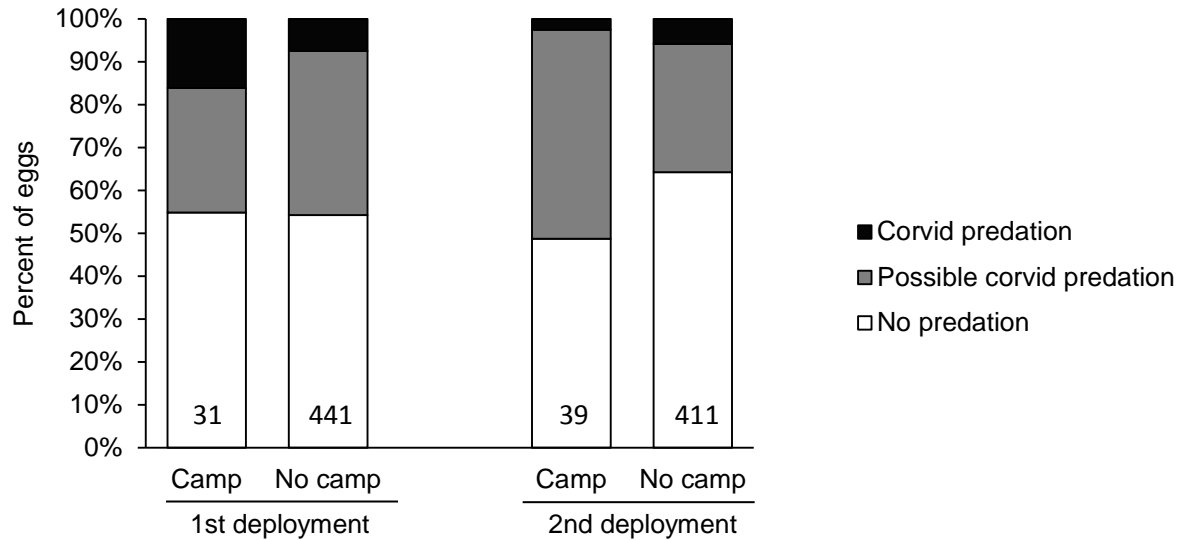


Figure 9. Proportion of eggs in three disposition categories, excluding unknown disposition, after first and second deployments of murrelet-mimic eggs in campgrounds (Camp) and outside of campgrounds (No camp) in Butano State Park and Portola Redwoods State Park. Sample sizes shown inside bars. Predation categories are described in Table 1.

When assessing effects of campgrounds on jay populations surrounding these campgrounds, the distribution of predation scores differed between egg locations within 1 km of campgrounds and locations more than 1 km away from campgrounds in the first deployment ($\chi^2_2 = 31.93$, $P < 0.001$; Fig. 10). Using maximally inclusive measures, the proportion of murrelet-mimic eggs predated within 1 km of campgrounds was 43% less than in locations more than 1 km away ($\chi^2_1 = 28.177$, $P < 0.001$; Fig. 10). Using maximally stringent measures the proportion of predated murrelet-mimic eggs did not differ between locations within and outside of 1 km of campgrounds ($\chi^2_1 = 1.142$, $P = 0.235$; Fig. 10). In the second deployment, the distribution of predation scores did not differ between egg locations within 1 km of campgrounds and locations more than 1 km away from campgrounds ($\chi^2_2 = 2.799$, $P = 0.247$; Fig. 10).

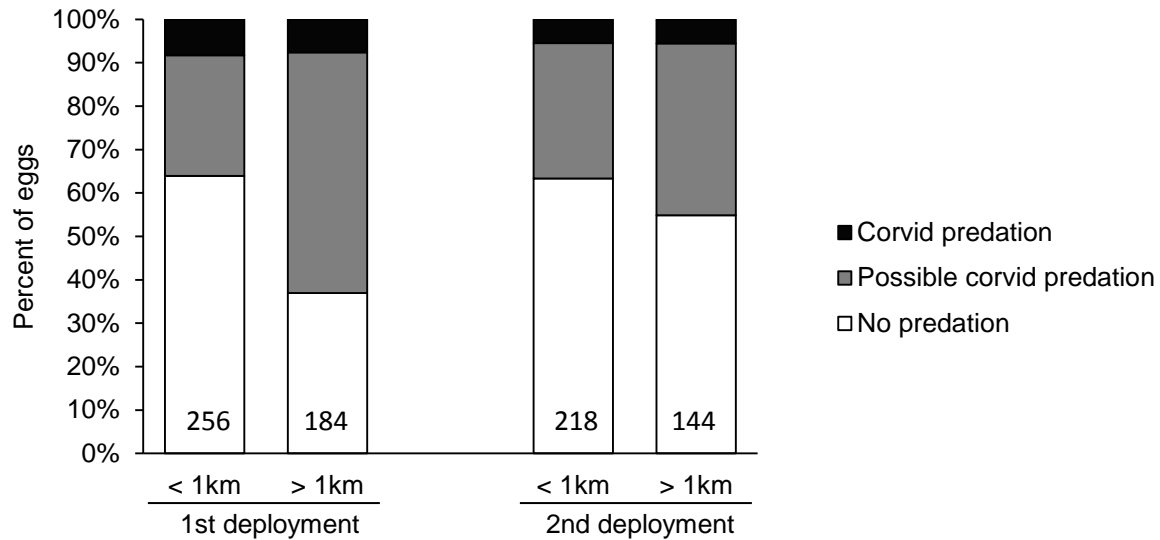


Figure 10. Proportion of eggs in three disposition categories, excluding unknown disposition, after first and second deployments of murrelet-mimic eggs within 1 km of campgrounds (< 1 km) and more than 1 km away from campgrounds (> 1 km) in Butano State Park and Portola Redwoods State Park. Sample sizes shown inside bars. Predation categories are described in Table 1.

Discussion

Deployment of murrelet-mimic eggs laced with carbachol in the forests surrounding high-visitor use areas of Butano State Park and Portola Redwoods State Park was effective at reducing predation by Steller’s jays on the murrelet-mimic eggs. The effectiveness of aversion achieved by the conditioning was similar to the effectiveness achieved in earlier field tests of this method in Redwood National Park (Gabriel and Golightly 2011). Here, we interpreted changes in predation between first and second egg deployments on murrelet-mimic eggs only, without comparison to simultaneously deployed control eggs as previously reported by Gabriel and Golightly (2011) for Redwood National Park. Using the most rigorous analysis criteria (14 to 35 day egg revisitation and assessment interval) and maximally inclusive assumptions (where all possible corvid predation was included in comparisons), we detected a decrease in predation of 44% in the central California parks. Maximally stringent assumptions (where possible corvid predation was excluded from comparisons) suggested a predation decrease of 80%. The actual effect may have been somewhere in between the two estimates.

The range of CTA effectiveness in central California parks (44 to 80%) was derived under similar egg revisitation criteria as was used in the Redwood National Park study. Gabriel and Golightly (2011) reported an equivalent decrease of 27 to 63% in predation on mimic eggs only

(for inclusive and stringent assumptions, respectively). However, the true effect of CTA estimated for Redwood National Park was based on comparison to control eggs (37 and 72% decrease in predation on mimic eggs for inclusive and stringent assumptions, respectively; Gabriel and Golightly 2011). This latter effect was stronger than the effect suggested by change in predation on murrelet-mimic eggs only. This difference was likely due to treatment affecting predation on mimic eggs within the first deployment; 25% of mimic eggs, but only 12% of entire egg pairs (consisting of one murrelet-mimic and one control egg each) in the Redwood National park study had remained unpredated during the first deployment (Gabriel and Golightly 2011). An additional indicator of observed treatment effects in the first deployment data was that attack rates on murrelet-mimic eggs were 12% less than attack rates on control eggs during the first deployment (Gabriel and Golightly 2011). This implied that jays were encountering multiple egg pairs within their territory, and subsequently they had already been conditioned on the next encounter within the first deployment. Effectiveness measured by decreases in predation on mimic eggs only between the first and second deployments thus likely underestimated the true CTA effect in the Redwood National Park study (Gabriel and Golightly 2011). This is probably also true for central California.

Forty-nine percent of mimic eggs were not predated in the first deployment. This implied that the deployment density of eggs may have been much greater than necessary to ensure that all jays were exposed. Similar to predation patterns reported by Gabriel and Golightly (2011) during the first deployment in Redwood National Park, at least a proportion of unpredated mimic-eggs in the first deployment was probably due to jays encountering multiple egg pairs within their territory. Subsequently they had already been conditioned on the next encounter. However, since no control eggs were used here, alternative explanations are also possible. The density of jays in central California parks may have been so low that almost half of the deployed eggs were not encountered by any jays. This seems highly unlikely. Gabriel and Golightly (2011) estimated a density of 7 jay pairs per 100 ha for their undeveloped study area in Redwood National Park, while others (W. Goldenberg, L. George, and J. Black, unpublished data) estimated 12 pairs per 100 ha surrounding a nearby campground in the same park. Thus the density of jay pairs for the deployment area surrounding highly developed campgrounds of the central California parks would have to have been considerably less than these numbers in order to result in so many unpredated eggs. A second alternative was that the proportion of jays that did not consume eggs at all (see Appendix in Gabriel and Golightly 2011) may have been substantially smaller in this geographic region than in Redwood National Park. This potential explanation could not be evaluated with the present data, but no evidence suggested that jays in the central California parks should be less likely to consume bird eggs than in northern California. Importantly, under

either alternative explanation the significant decrease in corvid predation on mimic eggs between the first and second deployments in conjunction with the large proportion of unpredated mimic eggs in the first deployment suggested that the CTA successfully treated all or most egg predating jays in the deployment area. Further, there is the potential to treat all jays in the central California parks with substantially smaller densities of egg deployment than used here.

The majority of unpredated mimic eggs in the first deployment were located within 1 km of campgrounds (where coincidentally egg density was greatest). By contrast, in areas more than 1 km away from campgrounds only 37% of mimic eggs were not predated in the first deployment. This coincided with about twice the deployment density of eggs within a 1 km radius around campgrounds compared to areas outside that radius (see Fig. 3). The discrepancy in deployment densities resulted from the logistical use of roads and trails for egg deployment where campgrounds were surrounded by a greater density of trails in the central California parks. Thus, the frequency of unpredated mimic eggs in the first deployment was greatest in areas of the greatest egg densities. This supports the interpretation that the large frequency of unpredated eggs in general, and specifically in areas close to campgrounds, was due to jays encountering multiple egg pairs within their territory, and subsequently avoiding eggs because they had already been conditioned on the next encounter. Thus, the effect of treatment we could measure by the decrease in egg predation between the first and second deployments by itself likely underestimated the true effect that was achieved.

During the second deployment, proportionally more eggs were predated within campgrounds than outside of campground boundaries. Since this rise in predation was due to an increase in eggs being classified as possibly corvid predated, it was likely due to both more Steller's jay predation and possibly more predation by rodents or other non-target species. Campgrounds in the central California parks opened for visitors between 1 March and 1 April. Thus the increase in egg predation in the campgrounds coincided with a large increase in the availability of anthropogenic food, attracting corvids and other wildlife foraging on these foods to the campgrounds. Data from our trail cameras and from incidental observations also suggested that prior to the final predation assessment the Steller's jays population included newly fledged jays (which were not conditioned). Jay parents travelling with young fledglings, as well as independent juveniles that do not have established territories may travel longer distances than territorial jays during the breeding season; these untreated jays may aggregate at profitable food sources such as campgrounds (Gabriel & Black 2008; W. Goldenberg, L. George, and J. Black, unpublished data). Thus, jays predating mimic eggs in campgrounds during the second deployment likely encountered mimic eggs for the first time. Retaining the use of a second

deployment into the future to complete the exposure of temporally and spatially distributed corvids living throughout the parks and adjacent lands seems prudent.

Data from trail camera pictures suggested that loss of mimic-eggs to non-corvid wildlife was not substantial. Eighty-eight percent of wildlife interactions captured by trail cameras showed Steller's jays. Classification of eggs that were missing or that showed sign of unknown predators (i.e. the majority of predated eggs, see Table 2) as 'possibly corvid predated' seemed therefore appropriate. Among other known egg predators, squirrels and foxes interacted with eggs, although apparently not in large numbers. Eggs that showed sign of possible rodent predation (chewed edges) or any other unknown predation could have been predated by jays before or after other wildlife interacted with the eggs. In addition, series of trail camera photographs documented that jays were capable of prying whole eggs off their attachment. Also, jays have been documented to carry a murrelet egg away from the nest after first puncturing it and eating egg contents (Golightly and Schneider 2009).

It is important to note that gray foxes, ground squirrels, and other small mammals are not likely to be found in the upper canopy where real murrelet eggs are found. Aversive treatment of these incidental predators on mimic eggs was therefore not a goal of the CTA application, and the apparently relatively small number of eggs lost to these predators preserved effectiveness. The applied carbachol dose of 24 mg per egg had induced egg avoidance in Steller's jays without any mortalities or observable long-term ill effects (Gabriel and Golightly 2011). Steller's jays weigh on average 106 to 128 g (depending on subspecies, Greene et al. 1998) and are amongst the smallest egg predators in the forest. It is unlikely that the carbachol dose would have had adverse effects on any other avian egg-predators in the forest habitat. Thus, negative impacts on non-target wildlife were absent, or at least not detectable.

Management Recommendations

Currently large predation rates on murrelet nests in their southern breeding range (estimated to be up to 80%; Hébert and Golightly 2007, Golightly and Schneider 2009) may be reduced substantially by introducing CTA for murrelet eggs in resident corvid predators. In the central California parks, Steller's jays appear to be the vastly predominant corvid predator. No corvids other than Steller's jays were found to interact with mimic eggs. Not all individual jays represent a risk to murrelets (Gabriel and Golightly 2011). A technique such as CTA allows targeting specifically those individual predators posing a threat to the species of concern, and may be most appropriate in situations where removal or severe reduction of a native species such as jays is

difficult to achieve (e.g. jays are highly mobile and very abundant) or unacceptable (e.g. parks and preserves with mandates to conserve all species). This first large field treatment in central California demonstrated that behavioral training was possible over large landscapes. With an estimated decrease in predation of at least 44 to 80%, CTA can likely achieve the target reductions in corvid predation (40 to 70%; Peery and Henry 2010) to assist recovery of murrelets in this region.

Analysis of all available data, regardless of revisitation intervals after each egg deployment, largely underestimated CTA effects detected compared to only analyzing data collected within 14 to 35 days after deployments. Thus, revisitation intervals in future effectiveness monitoring should be narrowed for more accurate predation assessments. The most rigorous revisitation interval suggested by Gabriel and Golightly (2011) was 21 to 25 days after each deployment.

Because jays probably encountered multiple egg pairs within their territory, we suggest that a lesser egg density can be used in the future. Use of roads and trails as transects for egg deployment may be continued for ease of access, wherever possible. However, deployment can be modified to add transects parallel to back country trails which would decrease deployment density while increasing treatment area. At current treatment densities, CTA was a cost effective management method with \$80 / ha (assuming approximately 600 ha treated). Decreasing egg densities may reduce this cost further, but the use of transects in roadless terrain may offset some or all of the saved costs.

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