

**EXPERIMENTAL ASSESSMENT OF TASTE AVERSION CONDITIONING ON
STELLER'S JAYS TO PROVIDE POTENTIAL SHORT-TERM IMPROVEMENT OF
NEST SURVIVAL OF MARBLED MURRELETS IN NORTHERN CALIFORNIA**

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Summary

Excessive predation on eggs of Marbled Murrelets has been linked to poor recruitment of young into the murrelet population, especially in the California, Oregon and Washington populations. Corvids have been implicated as the most influential egg predators on murrelets. Fragmented forests provide the only remnant murrelet nesting habitats in California, but these forests also support a high population density of opportunistic corvids like Steller's Jays. This increases predation risk on murrelet eggs. Effective reductions of egg predation require manipulation of the population density or predation behavior of egg predators. We tested conditioned taste aversion techniques for Steller's jays, exposing jays to murrelet-colored and sized eggs that had been treated with carbachol. In laboratory tests on 28 temporarily captive jays, aversion conditioning effectively induced subsequent aversion to the murrelet-mimic eggs. Attack latencies on murrelet-mimic eggs compared to control eggs between the initial and repeat exposure increased by several hours, and the strength of aversion remained constant over the range of retention periods tested (8 weeks). Field trials were conducted on murrelet-mimic eggs and control eggs deployed across a systematic grid on a 428 ha area in murrelet breeding habitat in Redwood National Park. The percentage of murrelet-mimic eggs that were attacked by corvids in the effectiveness assessment (the second field deployment following initial treatment) was reduced by 37% to 72% (depending on assumptions regarding corvid predation) in comparison to control eggs. Attack rates on murrelet-mimic eggs were 12% lower than attack rates on control eggs during the initial deployment, suggesting that the density of egg deployment (1 murrelet mimic egg / 2 ha) resulted in many jays having multiple encounters with treated murrelet-mimic eggs within their territories (they were already aversely conditioned when encountering a second egg within the first period of exposure). We concluded that corvid predation on murrelet-colored eggs can be reduced significantly, and that an egg density of 1 treated mimic egg per 4 ha should be sufficient to treat all corvid territories within a forest. We suggest that conditioned taste aversion treatment maybe a very cost-effective emergency plan to improve reproductive success of murrelets in the Pacific Northwest region.

Introduction

Predation on nests of Marbled Murrelets (*Brachyramphus marmoratus*) appears to have dramatically increased in recent years in the southern murrelet breeding range. Murrelets probably evolved with heavy predation pressure on nests and possibly breeding adults, which is evidenced by highly cryptic plumage and behavior of both adults and chicks at the nest (Carter and Stein 1995, Nelson and Hamer 1995, Golightly and Schneider 2009). Due to fragmentation and deterioration of the residual patches of breeding habitat in old growth redwood forests, murrelets have been increasingly unable to be cryptic. In part, they may be forced to choose branches for nesting that afford less protective cover from potential predators (McShane et al. 2004). A related, but likely more important factor, is that murrelets nest close to natural gaps in the forest canopy due to their morphological constraints for flight when entering the nest (McShane et al. 2004). Changes in the landscape over the last fifty years caused such gaps to include many hard, anthropogenic forest edges. Those new edge habitats are high in structural diversity and usually close to human habitation or traffic; these edges attract a variety of predators by providing a wide array of new food sources. Generally high structural diversity and the availability of anthropogenic food sources in fragmented, human altered landscapes support a dramatically higher population density of opportunistic omnivores like Steller's Jays (*Cyanocitta stelleri*). This higher predator density occurs not only along edges but all throughout much of the current murrelet breeding habitat; this differs in comparison to simply structured, contiguous old growth forest. A species that depends to a large degree on crypsis to evade nest predation like the Marbled Murrelet is especially vulnerable to the elevated risk of detection due to greater predator density.

Steller's Jays are suspected to be responsible for the major proportion of egg predation on nests of Marbled Murrelets in northern California and Oregon (Hébert and Golightly 2007, Golightly and Schneider 2009). Jays are most successful and abundant in habitats that are rich in structural diversity, including anthropogenic and human altered environments (Marzluff et al. 2004, Marzluff and Neatherlin 2006). Jays are opportunistic nest predators, but do not rely on bird eggs as a major food source and therefore do not form search images for nests. However, because jays are regular food cachers, jays are likely to remember and return to highly rewarding feeding sites such as masting trees, berry patches, bird feeders or compost piles. Returning to

rewarding sites does not apply to predation at most bird nests because passerines (the predominant victims of nest predation by jays) do not typically reuse old nests. There is mounting evidence however that Marbled Murrelets, like most alcids, repeatedly return to the same tree, even the same nest branch, for subsequent breeding attempts (Nelson and Peck 1995, Nelson 1997, McShane et al. 2004, Hébert and Golightly 2006, Golightly and Schneider 2011). Recent evidence from video at a murrelet nest suggests that jays preying on a murrelet egg were experienced and behaved in a systematic pattern that successfully removed the incubating parent from the egg; subsequently the jays opened and ate the egg (Golightly and Schneider 2009). Thus, individual territorial jays may remember and return to murrelet nests that they have previously preyed upon. Alternatively or possibly in addition to repeated predation, increase in jay densities may have significantly reduced jay territory sizes such that the risk of an encounter with a murrelet nest during the 28 day incubation period is quite great. Steller's Jays are moderately territorial, with the least amount of territorial overlap and intrusion tolerance during the breeding season (Brown 1963, Gabriel and Black 2007). Thus it is likely that a subset of the jay population is responsible for a high proportion of the loss of murrelet eggs and can be targeted for short term management strategies. More long term management actions should aim at a sustained reduction of jay abundances in murrelet habitat through the restoration of normal ecological processes, for example by prescribed episodic burns resulting in removal of the dense understory that provides nest sites and food sources for jays (Golightly and Gabriel 2009). However, until a sustained reduction of jay densities can be achieved, short term efforts are needed to reduce jay predation on murrelet eggs.

One possible short term management action would be the culling of territorial jays. However, this would upset the relatively stable territorial structure of a resident Steller's Jay population and likely result in a temporary influx of even greater densities of jays attempting to occupy the territorial vacancies. Lethal removal could be counter-productive by increasing the chance of incidental predation on murrelet nests (Draulans 1987, Reynolds et al. 1993, Cox et al. 2004). However, modifying the behavior of a resident predator population to avoid a specific food item through a non-lethal process called conditioned taste aversion (CTA) avoids the problems of lethal control by allowing the predator to remain in its ecological niche (Cowan et al. 2000, Cox et al. 2004). The stable, territorial social structure and long life expectancy of Steller's Jays presents a good opportunity for behavioral training of these nest predators to avoid

murrelet eggs in the future. To form a CTA an animal must ingest a harmful food item and associate the resulting illness after a single or small number of exposures with identity cues of that food (Nicolaus and Nellis 1987). The taste and associated cues such as color, size, shape or smell can all be used to identify a no longer desirable food item. CTA can be caused deliberately by administering an emetic, and has been successfully tested in a number of predator species for exploitation in non-lethal predator management (e.g. Nicolaus et al. 1983, Nicolaus and Nellis 1987, Conover 1990, Cox et al. 2004). Species that are suitable for CTA as a management tool should meet a list of minimum requirements as summarized by Nicolaus and Nellis (1987). Steller's Jays vary little in size, thus their meal size and dose of aversive agent received (per g body weight) will also be consistent. They feed on a variety of food items, and exploit bird eggs only as an incidental, non-essential food source. Notably, murrelet eggs are uniquely colored and relatively rare amongst eggs naturally occurring in the forest. Removal of murrelet eggs from the jay diet should therefore be relatively easy to achieve and very unlikely to result in food deprivation for jays. Finally, because jays defend territories, areas where aversions are established will be unlikely to receive a flow of new, unconditioned immigrants. Experiments on crows and other predators have shown the potential of CTA to reverse even robust food preferences and influence food selection for at least several months in free-ranging populations (Nicolaus et al. 1982, Nicolaus et al. 1983).

We experimentally tested a strategy for introducing conditioned taste aversion to murrelet eggs in resident jay pairs within known murrelet nest habitat. Our goals were to 1) establish a safe, effective aversive agent for application to wild Steller's Jays, 2) establish a retention time for the conditioned aversion by assessing repeated exposure to the eggs in temporarily captive jays, and 3) compare predation on treated and control eggs in a field experiment in murrelet nesting habitat. In the field experiment we assessed effectiveness of the CTA by comparing two consecutive exposures to treated and control eggs, several weeks prior and at the start of the murrelet nesting season. The effectiveness assessment allowed us to quantify the likelihood of protecting murrelet eggs.

Methods

Egg preparation

For captive experiments, raw, small-sized chicken eggs (26.4 ± 5.9 g; mean \pm SD) were washed and soaked for 5 min in food dye (green or red) mixed with vinegar for better shell penetration of the dye. Eggs that were presented during the first days of habituation phases were punctured immediately before presentation to the bird by pushing inward on the shell in an approximately 1 cm^2 area such that the fragmented shell remained on the surface of the egg contents (this helped determine whether a jay actually manipulated the egg).

Eggs for carbachol (carbamylcholine chloride, 99%, Acros Organics, Thermo Fisher Scientific, New Jersey, U.S.A.) dosage determination and CTA retention experiments were pierced at opposite ends and air was blown through one hole forcing the contents out through the opposite hole. One hole was then sealed with hot-glue (Surebonder DT-200 Dual Temperature Glue Gun and Glue Sticks; Ace Hardware Corp.). Control eggs were refilled with the egg contents, and sealed with glue. Contents of treated eggs were mixed with 0.32 or 0.24 ml (depending on dose) of a 100 mg carbachol / 1ml sterile water solution, injected back into the eggshell, and the remaining hole sealed with glue.

For field experiments, eggs were colored either in a blue-green hue closely resembling murrelet eggs (murrelet-mimic eggs), or red (control eggs). Irregular spotting as displayed on murrelet eggs was applied with dilute black acrylic paint to both colors. Murrelet-mimic eggs were pierced at opposite ends to extract contents. The contents were mixed with 0.24 ml carbachol solution, injected back into the eggshell, and the holes sealed with hot glue. Control eggs were spotted with glue at opposite ends to mimic the

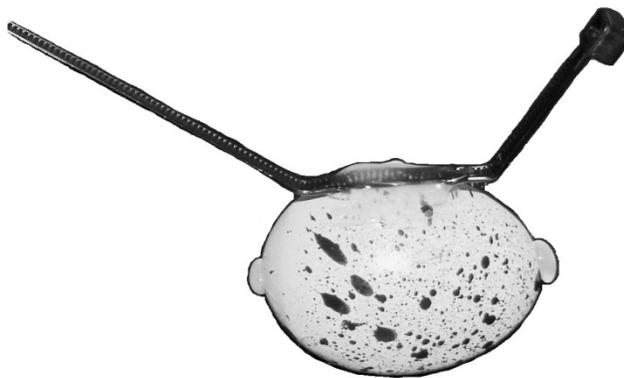


Figure 1. Small chicken egg painted to resemble Marbled Murrelet egg and glued to zip tie for field deployment in Redwood National Park.

appearance of glued murrelet-mimic eggs. 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 to all eggs along 2 cm of their widest side (Fig. 1).

Subjects for captive experiments

Wild Steller's Jays were captured in Eureka and McKinleyville, California between August 30, 2010 and March 3 2011, and temporarily housed in outdoor aviaries in the Humboldt State University Game Pens facilities. For ethical considerations, the number of birds captured and exposed to carbachol was kept at the minimum necessary to make statistically valid conclusions. We initially captured birds in groups of one to four and added new individuals only when necessary to replace birds that did not participate in experiments or to increase sample size to reach sufficient statistical power.

Birds received water ad libitum and were fed a maintenance diet of sunflower seeds and dry dog food during all times when they were not exposed to eggs. During all phases when eggs were presented, birds were housed in individual cages (4.5 m long, 2.6 m wide, and 2.3 m high) that were visually separated from all other experimental birds. Eggs were presented in 9 cm wide and 5 cm high, round plastic feeding dishes on cage floors, in the same manner that birds were accustomed to receiving their maintenance diet.

Jays were subjected to a habituation phase of three to seven days in captivity prior to experimental exposure to carbachol-treated eggs. Each bird received one small chicken egg for 8 hours per day during this habituation phase, alternating daily between green and red colored eggs. Jays were exposed to at least two punctured and one whole eggs during the habituation phase of captivity. Individuals who consumed eggs on at least two consecutive days and at least one whole egg were included in subsequent CTA experiments. Jays that failed these criteria were released back into the wild at the location of capture.

Egg attack during habituation phases and during experiments was scored on a scale from 0 (untouched) to 4 (contents consumed; Table 1). Eggs were weighed at the start and end of each experimental day to determine amount of egg consumed. Bird behavior and egg attack were

monitored every hour for 30 min until the end of experimental periods (8 hours for dosage experiments; 5 hours for retention experiments). We also determined latency to reach attack score 4 (attack latency) in 30 min increments. A maximum latency of total experimental time + 30 min was assigned to eggs that were never consumed. Results are reported as means \pm 1 SE, unless otherwise noted.

Table 1. Attack scores assigned to eggs during habituation and experimental phases in all laboratory tests of aversive conditioning with carbachol on temporarily captive Steller's Jays.

Score	Description of egg disposition
0	Egg untouched
1	Egg moved
2	Shell cracked, but too small for fluid loss
3	Shell broken open, but no visible consumption
4	Visible consumption of contents

Establishing dosage of an aversive agent

Carbachol is a widely available emetic that is water soluble, odourless and tasteless at doses known to be capable to produce CTA in birds (Cox et al. 2004, Nicolaus et al. 1989). Cholinergic agonistic emetics such as carbachol may have toxic effects at high dosage rates however, and repeated doses in short periods of time have potential to poison both target and non-target species (Conover 1990). It was therefore critical to identify an optimal effective dose that would induce a complete avoidance of treated eggs while also being sub-toxic to both targets and other animals that might be inadvertently exposed. In contrast, smaller doses of emetic, which cause only slight illness, could result in birds repeatedly sampling treated and untreated eggs. 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. Thus it is unlikely that the optimum dose for jays could have adverse effects on any other egg-predators in the forest habitat.

On day one of entering the carbachol dosage experiments (pre-treatment day) each bird was presented with two untreated eggs (containing no carbachol) for 8 hours. One egg was colored green and one was colored red. On the second day (treatment day) birds were presented with one egg treated with carbachol and painted in the color that had been selected by the bird on

day one (attacked exclusively or first; subsequently the attacked egg was described as “treatment-color”). After ingestion of treated egg contents, birds were monitored for behavioral responses (e.g. visible signs of illness such as bill wiping, salivation, vomiting, and diarrhea). On day three (post-treatment day) each bird was presented with the same choice of two eggs as on day one to determine whether birds changed their attack to eggs of a different color (response to the treatment). Birds participating in these experiments were monitored for health and behavioral changes for an additional 24 hours after last exposure to eggs and released on the fourth day after experimental start.

We began by testing a weight-specific dose that was equivalent to what had been effective at producing aversions in magpies (*Pica pica*, Prescott et al. 1997) and carrion crows (*Corvus corone*, Cox et al. 2004). Allometric scaling of this dose for adult Steller’s jays in the region (mean body mass: 115 g; from long-term banding data, P.O. Gabriel & J.M. Black, unpublished data) resulted in an initial carbachol dose of 32 mg per egg (1.03 ± 0.03 mg carbachol / g egg mass). We tested this dose on seven jays. We subsequently reduced the dose by 25% to 24 mg carbachol per egg (0.77 ± 0.03 mg carbachol / g egg mass), and tested it on five different individuals.

To assess the effect of carbachol treatment on egg attack by jays, we compared how attack measures (attack scores, amounts of egg mass consumed, and attack latencies) changed between pre-treatment and post-treatment days in treatment-color eggs compared to control-color eggs. We tested whether effectiveness differed between the two carbachol doses using two-factor ANOVAs where carbachol dose was the between-subjects variable.

Establishing CTA effects and retention times

After establishing 24 mg / egg as a safe, effective dose of carbachol for Steller’s Jays, we tested for how long a conditioned aversion to eggs treated with 24 mg carbachol was retained by jays. The main goal of this test was to allow us to determine a range of time for exposing jays to treated eggs in the subsequent field experiment, so that the time period of optimal aversion retention would overlap the murrelet egg incubation period in northern California. Jays that had

been exposed to a carbachol-treated egg were assessed on whether they remembered a conditioned aversion after a varying period of time (one to eight weeks), where in the intervening time they did not encounter any eggs at all.

On day one of CTA retention experiments (initial exposure), each bird was presented with either a green, carbachol-laced egg (0.73 ± 0.04 mg carbachol / g egg mass, treatment group, $n = 8$), or a green, untreated egg (control group, $n = 8$). Experimental exposure was limited to 5 hours because this had been found to be a sufficient time period to assess final attack scores on eggs, and minimized the amount of time birds were deprived of maintenance diet. After initial egg exposure, birds received only maintenance diet for a period of one to eight weeks. During each subsequent week up to eight weeks after exposure to the initial egg, one bird each from the treatment and control groups were presented with a green, untreated egg for 5 hours (post-treatment exposure). Birds were released back into the wild at the location of capture on the day following completion of post-treatment exposure.

To assess whether and for how long jays retained a conditioned aversion, we compared how attack measures (attack scores, amounts of egg mass consumed, and attack latencies) changed between initial exposure and post-treatment exposure for the treatment group compared to the control group. We used regressions to determine the rates of change over time in the two groups, and one-way ANCOVAs to determine whether these rates differed between the two groups, and whether the magnitude of change differed between the two groups.

Field assessment

Prior to the start of the murrelet nesting season (May-July), we deployed 214 Carbachol-laced, murrelet-colored and -sized eggs (murrelet-mimic eggs) and 214 untreated, red eggs (control eggs). These eggs were systematically placed throughout known nesting habitat of Marbled Murrelets in Redwood National Park between March 14 and April 6, 2011. Eggs were placed within 2 ha plots in a systematic grid covering a total area of 428 ha (Fig. 2). Within each plot, a tree was selected that provided a branch suitable for placing two eggs separated by 10 – 50 cm, and located in the sub-canopy below 10 m. Eggs were not placed in the redwood canopy to

ensure that our experiment did not attract jays to actual murrelet nest sites. Each selected sub-canopy tree received one murrelet-mimic egg and one control egg. Eggs were fastened to the branch with zip ties. If egg-pair locations were adjacent to roads or trails, a 4.5 m ladder was used to place eggs out of reach of humans. For egg-pair locations that were away from human traffic, the eggs were placed within reach of technicians from the ground.

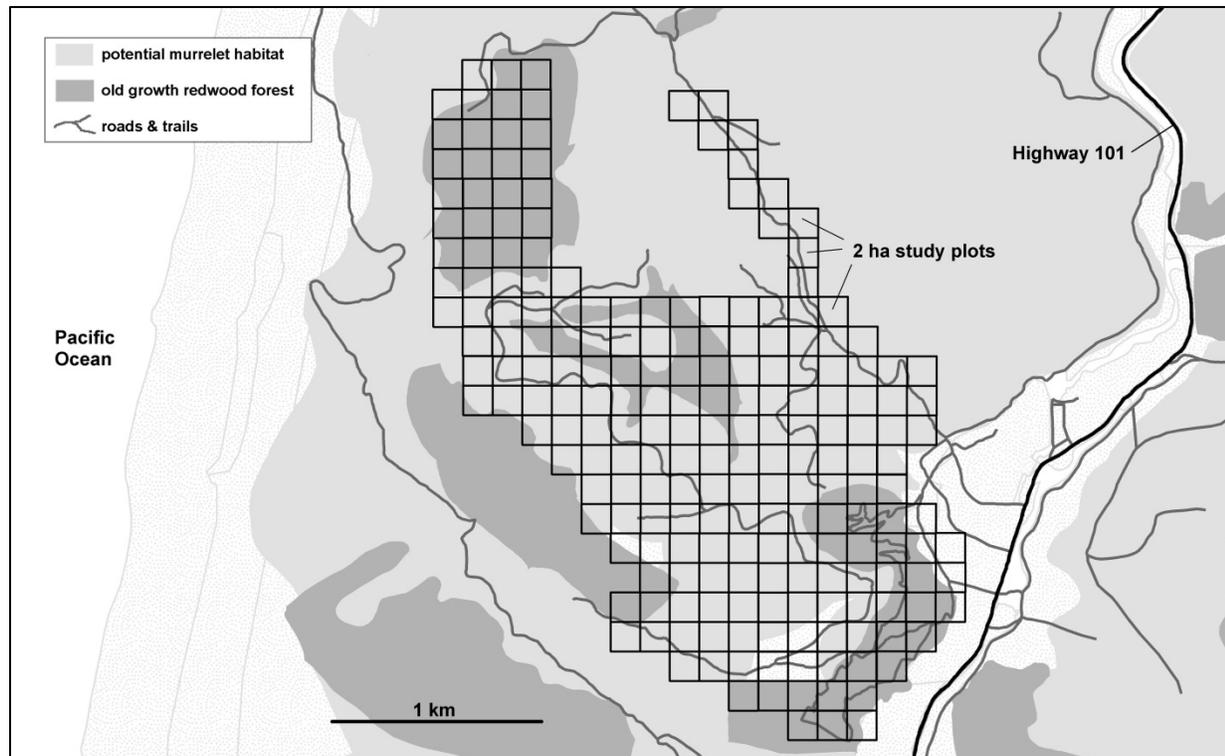


Figure 2. Study area for field deployment of murrelet-mimic and control eggs in Redwood National Park, California.

All locations were revisited 15 to 29 days after the first deployment to assess disposition of paired murrelet-mimic and control eggs. Disposition of eggs was scored on a scale from 0 to 1 based on the likelihood that they had been predated (Table 2). We visited 15 locations that had been visited within less than 23 days of the first egg deployment a second time. Two purposes were achieved by this second visit: We estimated how soon after deployment eggs were attacked, and we investigated whether assessment of attack that was made as much as a month after deployment accurately reflected initial predation. In the 12 locations where the second visit occurred within 35 days of the first egg deployment, the second visit resulted in the same

assessment of egg dispositions as the first visit. In the three locations where the second visit occurred more than 35 days later, it did not.

Table 2. Attack scores assigned to eggs after initial and repeat deployment of paired murrelet-mimic and control eggs in Redwood National Park for field tests of aversive conditioning with carbachol on wild Steller’s Jays.

Score	Description of score	Description of egg disposition
0	No predation	Egg is intact
0.5	Possible corvid predation	Egg shows sign of unknown predator, or egg missing while remains of paired egg are present
1	Corvid predation	Egg remains show conclusive signs of corvid attack
X	Bear predation	Both paired eggs missing, often accompanied by signs of bear presence

At the start of the murrelet nesting season (between May 16 and June 1, 2011) we repeated the deployment of murrelet-mimic and control eggs on the same set of trees as the first deployment. All egg-pair locations were again revisited 21 to 25 days after this second deployment to assess disposition of murrelet-mimic and control eggs. In addition, we used motion sensitive trail cameras at six plots during this second deployment to validate disposition scores.

The effectiveness of CTA in protecting murrelet-mimic eggs from predation was determined by comparing the predation rate of murrelet-mimic eggs to control eggs between the first and second egg deployment. We compared three indicators of change in predation of murrelet-mimic eggs: attack score of mimic eggs relative to paired control, proportions of predated mimic and control eggs, and likelihood of predation on mimic eggs relative to the location of other predated mimic eggs.

We tested whether attack scores of murrelet-mimic eggs relative to their paired control eggs changed between the first and second deployment using a Wilcoxon signed rank test for paired comparison of changes within the same egg-pair locations. Plots where both eggs were intact (not found by predators) or both eggs were missing (probable bear predation) after the first deployment, or where both eggs were missing after the second deployment were excluded from this comparison.

We used Chi-square tests to compare proportions of predated mimic and control eggs. First we examined whether predation differed between mimic eggs and control eggs within a deployment for the first deployment, and again for the second deployment. Then we examined whether predation differed between the first deployment and the second deployment for murrelet-mimic eggs, and again for control eggs. We used two different groupings of attack scores for these comparisons; for a maximally inclusive measure of corvid predation, eggs with scores 0.5 and 1 were categorized as predated, whereas eggs with score 0 were categorized as not predated (eggs predated by bears were excluded from comparisons); for a maximally stringent measure of corvid predation only eggs with score 1 were categorized as predated, eggs with score 0 were categorized as not predated, and eggs with score 0.5 or predated by bears were excluded from comparisons.

To assess whether all territorial jays in the study area had encountered experimental eggs, we examined whether corvid attacks were spatially clustered in each deployment. We used Getis-Ord G_i^* Hot Spot Analysis (ArcGIS 9.3; ESRI Inc., Redlands, California, U.S.A.) to determine whether egg-pairs that had been attacked by corvids (where at least one egg had received a score 1) or egg-pairs that had not been attacked by corvids (where no egg had received a score 1, excluding egg-pairs predated by bears) tended to be close to each other throughout the study area. For the purpose of this analysis we designated egg-pairs that had been attacked by corvids as 1, and egg-pairs that had not been attacked by corvids as 0. The analysis operated by assessing each egg-pair location within the context of neighboring egg-pair locations. If an egg-pair location's value was 1 (or 0), and the values for all or most of its neighboring egg-pair locations was also 1 (or 0), it was a part of a hot spot (or cold spot). The local sum for an egg-pair location and its neighbors was compared proportionally to the sum of all egg-pair locations; when the local sum differed from the expected local sum, and that difference was too large to be the result of random chance, a statistically significant z score resulted.

As an alternative spatial approach we tested whether the occurrence of corvid attacks in the second deployment changed with distance from egg-pairs that had been attacked by corvids in the first deployment. We measured the distances from each egg-pair location where at least one egg had received a score 1 in the first egg deployment to surrounding egg-pair locations

(within 500 m) that received at least one score of 1 in the second egg deployment. The proportion of egg-pairs with a score 1 was compared between egg-pair locations within 300 m (which included all the directly neighboring egg-pairs) and egg-pair locations between 300 to 500 m away in a paired t-test. Only egg-pair locations with at least 4 neighboring egg-pairs with viable data (i.e. enough neighboring egg-pair locations established and not bear predated) in each distance category were included in this analysis.

We assessed whether our calculated effectiveness of aversion conditioning differed between the interior and the edge of the study area. Edge plots were here defined as plots in which at least one side did not border on another plot containing an egg-pair; they were not usually located on actual forest edges. Interior plots were egg-pair plots that were surrounded on all sides by other egg-pair plots. T-tests were used to compare attack scores of murrelet-mimic eggs relative to their paired control eggs between egg-pairs located in edge plots and egg-pairs in interior plots for the first egg deployment, and again for the second deployment.

To investigate whether the aversion conditioning of jays was influenced by the location of treatment, we assessed whether the likelihood of attack on a murrelet-mimic egg changed with the distance to corvid predated murrelet-mimic eggs within each deployment, and between the first and second deployments. We measured the distances from each egg-pair location where the murrelet-mimic egg had received a score 1 to all surrounding egg-pair locations (within 500 m). The average attack scores of murrelet-mimic eggs relative to their paired control eggs were compared in paired t-tests between egg-pairs within 300 m and egg-pairs in a distance category of 300-500 m in paired t-tests. For all spatial analyses, observations where both eggs were missing (probable bear predation) were excluded from the data.

Results

Captive experiments

During habituation to eggs as a food source, 36% of 52 jays did not consume any eggs, 10% only consumed previously punctured eggs, and 54% consumed whole eggs. The number of jays interacting with eggs as a food source increased slightly after the first day, but did not subsequently change (Fig. 3). No long-term behavioral changes or mortalities following carbachol ingestion were detected, and all birds released back into the wild were subsequently resighted many days after release.

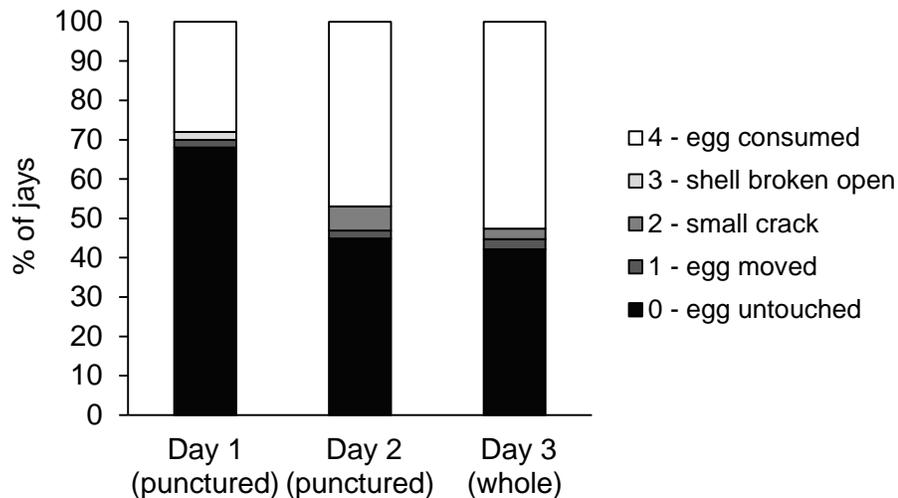


Figure 1. Distribution of attack (scores 0-4 assigned according to Table 1) by temporarily captive Steller's Jays on untreated eggs that were presented to birds either punctured or whole on the first three days of habituation.

Establishing dosage of an aversive agent

Attack by jays on treatment-color eggs compared to simultaneously presented control-color eggs decreased by 2.7 ± 1.1 score points when re-exposed to both types of eggs on day three ($F_{1, 23} = 5.53$, $P = 0.04$, Fig. 4a). There was no difference in the relative change of attack score between the two carbachol doses (24 mg: -3.2 ± 1.5 , 32 mg: -2.3 ± 1.6 ; $F_{1, 23} = 0$, $P = 1.00$). Amount of treatment-color egg mass consumed compared to control-color egg mass decreased

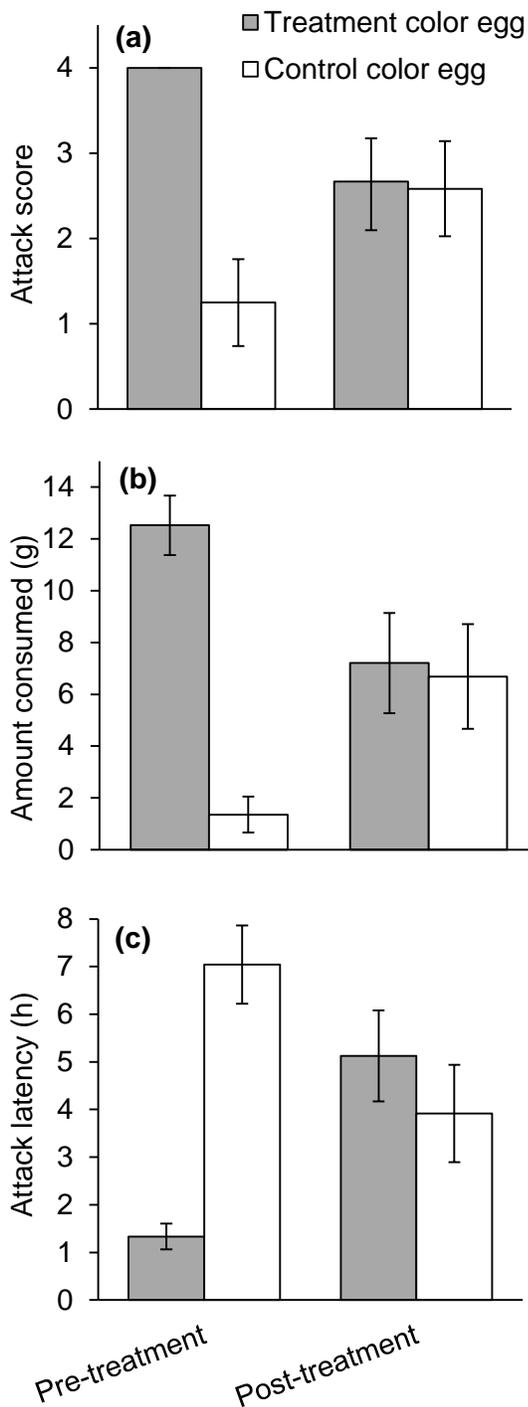


Figure 4. Egg attack by 12 Steller's Jays simultaneously presented with one treatment color egg and one control color egg. Mean attack score, amount of egg consumed, and attack latency before (Pre-treatment) and after (Post-treatment) consuming a treatment color egg treated with carbachol. Error bars denote ± 1 SE.

by 10.7 ± 3.5 g when jays were re-exposed to both types of eggs on day three ($F_{1,23} = 8.52$, $P = 0.015$, Fig. 4b). The 24 mg carbachol dose tended to have a slightly greater effect than the 32 mg dose (24 mg: -13.0 ± 3.8 g, 32 mg: -9.0 ± 5.6 g; $F_{1,23} = 4.34$, $P = 0.06$). Latency of attack on the treatment-color egg compared to the control-color egg increased by 6.9 ± 1.9 hours when re-exposed to both types of eggs on day three ($F_{1,23} = 12.01$, $P = 0.006$, Fig. 4c). There was no difference in the relative change of attack latency between the two carbachol doses (24 mg: $+8.4 \pm 2.5$ h, 32 mg: $+5.9 \pm 2.9$ h; $F_{1,23} = 0.05$, $P = 0.83$).

Establishing CTA effects and retention times

All jays in the treatment group except one individual completely avoided eggs during post-treatment exposure (i.e. attack score 0, 0g of egg consumed, and maximum latency assigned). Two jays in the control group also failed to consume eggs during post-treatment exposure. Changes in egg attack between initial and post-treatment exposure were constant across the range of one to eight week retention periods. Also, the rates of change over time did not differ between treatment and control groups (Table 3).

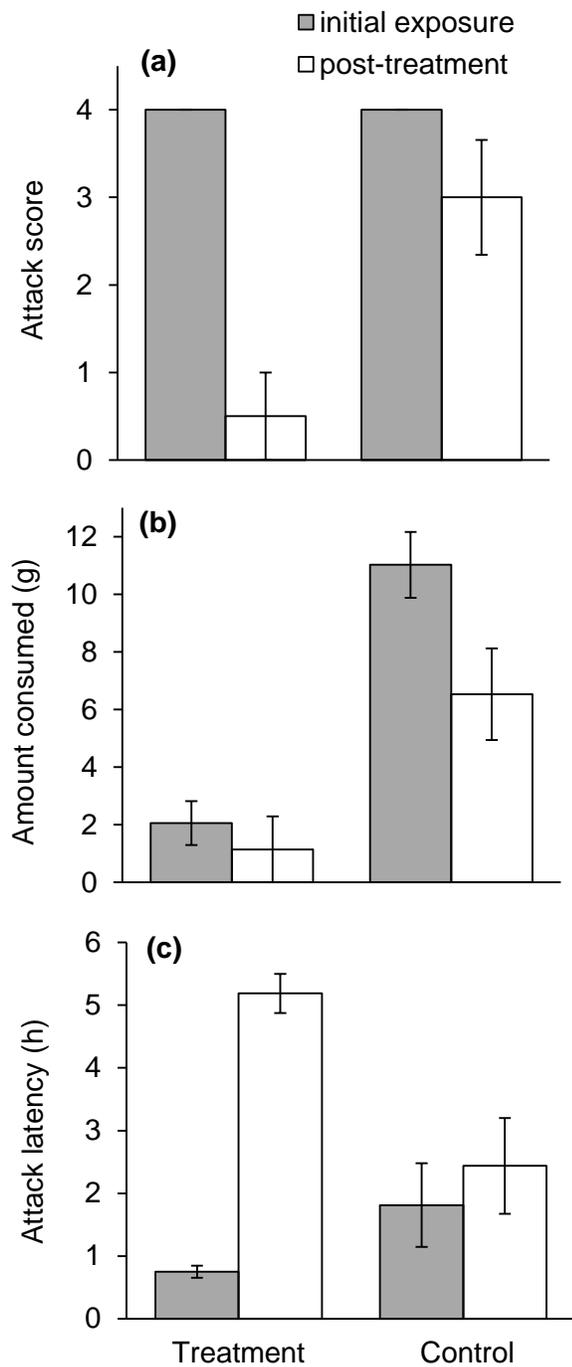


Figure 5. Egg attack by 8 Steller's Jays exposed to carbachol-treated eggs in initial exposure and untreated eggs in post-treatment exposure (Treatment), and 8 different jays exposed only to untreated eggs (Control) during both exposures. Mean attack score, amount of egg consumed, and attack latency during initial exposure and post-treatment exposure. Error bars denote ± 1 SE.

Attack scores of jays in the treatment group decreased by 2.5 ± 0.73 score points between initial exposure and post-treatment exposure when compared to jays in the control group ($F_{1, 13} = 10.85$, $P = 0.0058$, Fig. 5a).

The amount of egg consumed differed between jays in the treatment group and the control group by 9.0 ± 1.6 g during initial exposure ($F_{1, 13} = 39.3$, $P = 0.00003$; Fig 5b), and by 5.4 ± 1.4 g during post-treatment exposure ($F_{1, 13} = 8.09$, $P = 0.014$; Fig. 5b). It was not surprising that egg consumption of jays in the treatment group was already significantly lower in the initial exposure, because jays in the treatment group usually ceased feeding on carbachol-laced eggs after the first taste. Thus there was no difference between treatment group and control group in the change of the amount of egg consumed between initial exposure and post-treatment exposure (treatment group: -0.9 ± 1.4 g, control group: -4.5 ± 2.1 g; $F_{1, 13} = 2.05$, $P = 0.176$; Fig. 5b).

Attack latency of jays in the treatment group increased by 3.8 ± 1.0 hours between initial exposure and post-treatment exposure compared to jays in the control group ($F_{1, 13} = 13.73$, $P = 0.0026$, Fig 5c).

Table 3. Change over 8 weeks in the difference between egg attack at initial exposure and egg attack at post-treatment exposure for 8 Steller’s Jays exposed to carbachol-treated eggs in initial exposure and untreated eggs in post-treatment exposure (Treatment group), and 8 different jays exposed only to untreated eggs (Control group) during both exposures. Rates of change in the difference of attack score, amount of egg mass consumed, and attack latency are reported for the treatment and control groups, and also the difference in the rates of change between treatment group and control group.

	Rate of change over 8 weeks			Difference in rates of change		
	r ²	n	P	F	n	P
Attack score						
Treatment group	0.17	8	0.31	0.17	16	0.69
Control group	0.25	8	0.20			
Amount consumed						
Treatment group	0.24	8	0.22	0.08	16	0.78
Control group	0.04	8	0.64			
Attack latency						
Treatment group	0.07	8	0.52	0.55	16	0.47
Control group	0.05	8	0.59			

Field assessment

In the first egg deployment, 19% of egg-pair locations were likely predated by bears. Among the remaining locations, 88% were likely found by corvids. In the second field deployment, 45% of locations were likely predated by bears. Among remaining egg-pair locations, 91% were likely found by corvids (Table 4). Attack scores of murrelet-mimic eggs relative to their paired control eggs decreased by 0.33 ± 0.07 score points between the first and second egg deployment within the same egg-pair locations (Wilcoxon’s $W = 380.5$, $n = 61$, $P < 0.001$; Table 4).

Using maximally inclusive measures (scores 0.5 and 1 were used to signify corvid attack, see Fig. 6), the overall proportion of predated murrelet-mimic eggs was 12% lower than the overall proportion of predated control eggs in the first deployment ($X^2 = 5.22$, $P = 0.02$), and 37% lower in the second deployment ($X^2 = 29.93$, $P < 0.00001$). The overall proportion of murrelet-mimic eggs attacked in the second deployment was 27% lower than in the first deployment ($X^2 = 13.41$, $P = 0.00025$), but the proportion of control eggs attacked did not differ between first and second deployments ($X^2 = 0.26$, $P = 0.61$).

Table 4. Disposition of paired eggs after initial and repeat egg deployments of murrelet-mimic eggs and control eggs in Redwood National Park. n denotes number of egg pairs, proportion denotes proportion of egg pairs in relation to total number of egg pairs deployed excluding pairs likely predated by bears. Scores assigned according to Table 2.

Predation outcome (attack score)	Initial deployment		Repeat deployment	
	n	proportion	n	proportion
<i>Mimic egg predated by corvid (1)</i>	50		13	
Paired Control egg predated by corvid (1)	16	0.09	4	0.03
Paired Control egg possibly predated by corvid (0.5)	34	0.20	9	0.08
Paired Control egg not predated (0)	0	0	0	0
<i>Mimic egg possibly predated by corvid (0.5)</i>	81		51	
Paired Control egg predated by corvid (1)	13	0.07	17	0.15
Paired Control egg possibly predated by corvid (0.5)	63	0.36	29	0.25
Paired Control egg not predated (0)	5	0.03	5	0.04
<i>Mimic egg not predated(0)</i>	43		53	
Paired Control egg predated by corvid (1)	4	0.02	15	0.13
Paired Control egg possibly predated by corvid (0.5)	18	0.10	28	0.24
Paired Control egg not predated (0)	21	0.12	10	0.09
<i>Total egg pairs not predated by bears</i>	174		117	
<i>Total egg pairs predated by bears</i>	40		97	
<i>Total egg pairs deployed</i>	214		214	

Using maximally stringent measures (only score 1 used to signify corvid attack, see Fig. 6), the overall proportion of predated murrelet-mimic eggs did not differ from the overall proportion of predated control eggs in the first deployment ($X^2 = 0.07$, $P = 0.79$), but was 72% lower in the second deployment ($X^2 = 30.61$, $P < 0.00001$). The overall proportion of murrelet-mimic eggs attacked in the second deployment was 63% lower than in the first deployment ($X^2 = 18.73$, $P = 0.00002$), but the proportion of control eggs attacked did not differ between first and second deployments ($X^2 = 2.51$, $P = 0.11$).

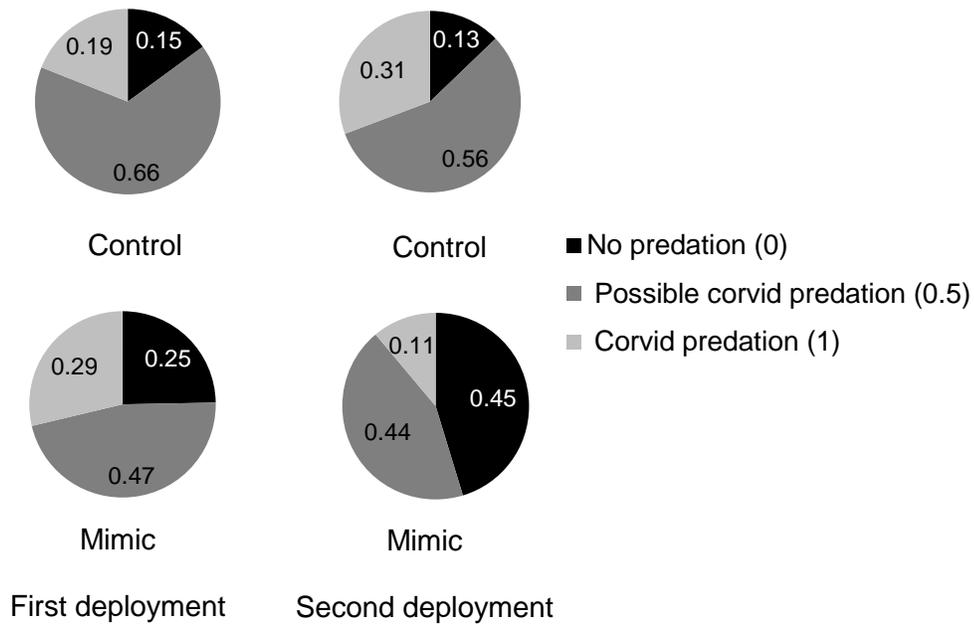


Figure 6. Proportion of eggs in three disposition categories, excluding bear predations, after first (n = 174) and second deployments (n = 117) of murrelet-mimic eggs (Mimic) and control eggs (Control) in Redwood National Park. Scores described in Table 2.

Corvid predation on experimental egg-pairs showed very little clustering. In the first deployment only 2 hotspots (where predated egg-pairs were closer to other predated locations than expected by chance), containing 10 and 9 egg-pairs respectively, were identified. In the second deployment only 4 hotspots, containing 5, 3, 1 and 1 egg-pairs respectively, were found. With the exception of the two single egg-pair hotspots in the second deployment, all these hotspots were located along the edge of the study area, where the effects of the small number of neighboring locations on the local sum were unproportionately large. No cold spots (where egg-pair locations not predated by corvids were closer to other unpredated locations than expected by chance) were identified in either deployment. The proportion of corvid attacks in the second deployment did not change with distance from egg-pairs that had been attacked by corvids in the first deployment (proportion difference between distance categories $x < 300$ m and 300 m $< x < 500$ m: 0.03 ± 0.03 ; $t_{52} = 0.76$, $P = 0.45$).

Attack scores of murrelet-mimic eggs relative to their paired control eggs did not differ between the interior and the edge of the study area in the first egg deployment (mean attack score edge: 0.02 ± 0.05 ; mean attack score interior: -0.01 ± 0.03 ; $t_{172} = 0.46$, $P = 0.65$). Relative egg predation did also not differ between interior and edge in the second egg deployment (mean attack score edge: -0.21 ± 0.06 ; mean attack score interior: -0.30 ± 0.05 ; $t_{115} = 1.09$, $P = 0.28$).

Mean attack scores of murrelet-mimic eggs relative to their paired control eggs did not change with the distance to corvid predated murrelet-mimic eggs. This was the case regardless whether the effect was investigated within each egg deployment or between first and second deployments (attack score difference between distance categories $x < 300$ m and $300 \text{ m} < x < 500$ m: mean = $0.002 - 0.03$; $t = 0.10 - 0.76$, $n = 13 - 50$, $P = 0.45 - 0.92$).

Discussion

Trace quantities of carbachol injected into eggs were effective in reducing predation by Steller's Jays on eggs similar in size, shape and coloration to murrelet eggs. Doses of 24 and 32 mg of carbachol per egg, equivalent to an available dose of 209 and 278 mg / kg body mass for an average adult jay in our study region, effectively reduced the likelihood of attack and the amount of egg contents jays consumed (although actual ingested dose was only a fraction of the available dose). Most significantly, aversion conditioning increased attack latencies in the laboratory by several hours on eggs that resembled previously encountered treated eggs. The strength of aversion remained constant over the eight week retention period that was tested.

In the wild, birds are not confronted with the choice of either eating an egg provided in a constrained space or not eating anything for many hours, as in our laboratory tests. An attack latency of several hours in the laboratory likely means that jays in the wild would ignore a murrelet-mimic egg that they find after they have been taste-aversion conditioned. Wild crows conditioned to avoid eggs of a certain color have been found to abandon sites where eggs of this color were offered, and foraged elsewhere (Nicolaus et al. 1983). Jays remembered and avoided eggs that resembled previously encountered treated eggs for a period of at least two months. This result is similar to studies on other avian and mammalian predators where aversions were retained for periods of at least 7 to 12 months (Nicolaus et al. 1982, Dimmick and Nicolaus 1990, McKay et al. 1999), also equivalent to the maximum retention periods tested in these studies. Thus, aversion conditioning with carbachol has the potential to protect the targeted prey item at least for an entire breeding season and likely longer.

An important difference between most unsuccessful studies of CTA and our study is the use of an aversive substance that is undetectable to the predator during ingestion of the bait. Eggs containing carbachol were initially consumed freely, but within minutes feeding stopped abruptly and was followed by symptoms of illness such as salivation, bill wiping, vomiting and diarrhea. Following this experience, jays ceased or dramatically reduced predation on the referent egg type, even when it was subsequently encountered untreated. Thus, jays apparently associated the experienced illness with the food item itself. By contrast, aversive agents that are detectable to predators by taste or smell upon first encounter tend to induce avoidance of treated bait items

only. In the latter case, predators seem to associate illness with the smell or taste of the aversive substance and quickly learn to distinguish treated from non-treated referent food items (Burns 1980, Ellins & Martin 1981, Avery & Decker 1994). In our study, jays probably associated the unique coloring with the illness.

A second important factor for the success of aversion conditioning is the relative importance of the prey item in the predator's diet. Eggs (especially murrelet eggs) are a rare and opportunistically procured food item for Steller's Jays (Vigallon & Marzluff 2005). Our finding that only slightly more than half of the jays presented with eggs in a captive situation reliably recognized and preyed on eggs even before aversive conditioning is consistent with this assessment. Removing eggs from a jay's diet through CTA, especially eggs of a rarely encountered prey species like the Marbled Murrelet, should thus not interfere with a jay's ability to meet its nutritional needs and should be relatively easily achieved. Indeed, even jays that initially freely preyed on eggs quickly ceased or dramatically reduced predation on eggs similar to those encountered during conditioning, increasing consumption of alternative food instead. By contrast, aversive conditioning of predators with the goal to avoid common prey items, such as kestrels (*Falco sparverius*) preying on young birds (Nicholls et al. 2000), or coyotes (*Canis latrans*) preying on sheep (*Ovis aries*; Burns 1983), has been found to be largely ineffective. A likely factor in these failures is the energetic cost of avoidance of the prey item to the predator.

Both carbachol doses we tested, 24 and 32 mg per egg, were equally effective in inducing aversions in jays. Symptoms of illness from carbachol ingestion were usually observable within only a few minutes of jays sampling egg contents. We could visually confirm vomiting for a smaller proportion of jays that had received eggs containing 24 mg of carbachol (7 out of 13) compared to jays that had received eggs containing 32 mg of carbachol (5 out of 7). However, jays that had received the 24 mg dose reduced their attacks on the previously treated egg type just as effectively, and even tended to consume less content of this egg type than jays treated with 32 mg carbachol. Evidence from CTA tests on some mammalian predators suggests that concentrations of aversive agent that do not produce vomiting, but cause prolonged nausea, can establish aversion that may sometimes exceed the effectiveness of doses that induce vomiting every time (Gustavson and Garcia 1974; Colvin 1975; Burns 1980). In addition to optimal effectiveness in inducing aversion, the lower dose of 24 mg carbachol per egg allows greater

cost-effectiveness of large-scale treatment, and less environmental exposure of a potentially toxic chemical. The appropriateness of our decision to use 24 mg of carbachol per egg for retention tests in captivity and field experiments was confirmed through continued effectiveness of the dose in inducing aversions in these tests.

Field tests with carbachol-treated murrelet-mimic eggs in murrelet breeding habitat confirmed that effectiveness of the CTA technique developed in captivity was transferrable to free-ranging jays; resident corvids were successfully conditioned to avoid murrelet-mimic eggs. Steller's Jays were most likely the predominant corvid predator attacking experimental eggs. Jays were resident throughout the study area at a density of approximately 7 pairs / 100 ha, or 30 pairs in the entire 428 ha study area (W. Goldenberg, L. George, and J. Black, unpublished data). However, common ravens (*Corvus corax*) are also resident in this area, with one to two pairs expected to use the study area (Scarpignato 2011). Three instances of ravens preying on experimental eggs in three different locations, documented by motion-sensitive trail cameras during the second egg deployment, confirmed that ravens were responsible for some corvid attacks on experimental eggs. Eggs that had been predated by ravens were not distinguishable by subsequent visual inspection from eggs predated by Steller's Jays. However, since ravens occurred in low densities, and rarely used old-growth stands in Redwood National Park (Bensen 2008, Scarpignato 2011), we assumed the relative predation by ravens on experimental eggs to be much lower compared to predation by Steller's Jays. Moreover, in all instances where ravens were photographed preying on experimental eggs during the second egg deployment, only control eggs were attacked. Therefore we infer that these ravens probably experienced treated eggs during the first deployment. Carbachol treatment had an overall strong effect on corvid predation, reducing corvid attacks on murrelet-mimic eggs by 37 to 72% compared to control eggs. Thus, the tested carbachol dosage of 24 mg per egg seemed to effectively induce aversions in jays and ravens alike.

Corvids continued to prey on control eggs during the second egg deployment at the same rate as during the first deployment. In contrast, jays in captivity that had a choice between treatment-color eggs and control eggs after they had encountered a treated egg increased predation on the "safe" control eggs. The discrepancy in these outcomes is likely due to jays in captivity shifting feeding to the only other available food, in this case control-color eggs. This

compensatory predation is commonly observed in similar captive experiments for taste aversion conditioning (for example in crows, Cox et al. 2004, and magpies, Prescott et al. 1997). In the wild, conditioned animals are not similarly constrained, and can instead quickly continue feeding on other foods, sometimes even extending the avoidance to less similar food items like eggs of a different color (Nicolaus and Nellis 1987, Dimmick and Nicolaus 1990). Similarly, wild jays did not compensate for the lost opportunity of predating murrelet-mimic eggs by increasing predation on control eggs, although the two egg-types were found in immediate proximity. Thus, it is highly unlikely that jays in the wild might increase their predation on other bird eggs in response to conditioned avoidance of murrelet eggs.

The great majority of experimental eggs (88 – 91% of egg-pair locations that had not been predated by bears) were found by corvids. Egg-pairs that were first visited after two to three weeks from the first deployment were found in the same disposition upon the second visit (up to 35 days after the first deployment), but eventually disappeared two to three months later. Thus, corvids discovered experimental eggs within days to few weeks of deployment and before eggs could spoil. Although home ranges of jays in the study area encompassed on average 16 ha, and overlap between resident pairs was minimal in core use areas of their home ranges (W. Goldenberg, L. George, and J. Black, unpublished data), jays seemed to spend enough time traveling their entire territory to find most egg-pairs. This discovery rate was likely facilitated by jays spending more than half of their time in the low canopy below 10 m, where our experimental eggs were placed, compared to less than half their time spent in the mid and upper canopy combined (W. Goldenberg, L. George, and J. Black, unpublished data). In addition, the overall even distribution of corvid attacks across the study area suggests that the intensity of our CTA did not miss resident corvids in the area. Attack rates on murrelet-mimic eggs were already 12% lower than attack rates on control eggs during the initial deployment, suggesting that the density of egg deployment (1 murrelet mimic egg / 2 ha) resulted in many jays repeatedly encountering several treated murrelet-mimic eggs within their territories; thus all of our estimates probably underestimate the potential for conditioned taste aversion, and we expect treatment to be effective even at considerably lower egg densities.

A small number ($n = 13$) of murrelet-mimic eggs were still predated by corvids during the second deployment. This indicates that despite the high discovery rate of eggs, some corvids

may not have been exposed to treated eggs during the first deployment. Individuals may have been missed by the first treatment where bears predated egg-pairs (a total of 40), pre-empting for example one of two partners in some pairs that shared a territory, or non-territorial birds that used much larger home ranges (W. Goldenberg, L. George, and J. Black, unpublished data). Additionally, some jays overlapping the study area only on the edge may have not encountered eggs initially. Thus, if the corvid predation events on murrelet-mimic eggs during the second deployment represent first exposures for some corvids, then the use of at least two consecutive deployments to compensate for loss of eggs to non-corvid predators seems prudent, especially if the treated area includes a large proportion of edge area.

The relative likelihood of a murrelet-mimic egg to be predated did not change with the distance of this mimic egg to other corvid predated mimic eggs. Thus, the effect of conditioning that was achieved by the carbachol treatment of murrelet-mimic eggs was independent from the location of the conditioning. Similarly, other studies showed that avoidance that resulted from experienced illness was much more likely to be associated with food items than with locations or other non-food cues (Garcia & Koelling 1966; Nicolaus et al. 1983). It therefore seems reasonable to assume that the CTA will transfer to real murrelet eggs that jays may encounter elsewhere in the canopy. Murrelet eggs within breeding territories of jays and ravens are likely to be additionally protected because territories are defended against incursions of untreated conspecifics, especially during breeding (Brown 1963; Nicolaus 1987). As long as the same individuals inhabit a region, the duration of conditioned aversion effects may thus exceed the span of time that murrelet eggs are vulnerable to depredation (Dimmick & Nicolaus 1990).

Conditioned taste aversion using mimic eggs treated with 24 mg carbachol may be a very effective technique to reduce jay predation on Marbled Murrelet eggs. Currently high predation rates on murrelet eggs in their southern breeding range (estimated to be up to 80%; Hébert and Golightly 2007, Golightly and Schneider 2009) may be reduced by 37 to 72% (equivalent to reduction of corvid attacks on murrelet-mimic eggs compared to control eggs) by introducing CTA for murrelet eggs in resident corvid predators. Thus, a currently low hatching success of for example 25% could be improved to minimally 53%, or as much as 79%. For large scale use of CTA as a management tool, the methods in this study can be modified for logistical and cost-efficiency. For management actions, the use of control eggs is usually unnecessary; although it

remains a measure of effectiveness. Based on large, minimally overlapping jay home ranges and high detection rates of experimental eggs measured in this study, we suggest that a deployment density of approximately 1 carbachol-treated murrelet-mimic egg per 4 ha would efficiently introduce CTA for murrelet eggs in a resident corvid population in the Pacific Northwest. For ease of access, roads and trails may be used as transects for egg deployment wherever possible. Since density of roads and trails will be greater in areas of high recreational use, a deployment method relying primarily on roads and trails would result in a greater density of deployed treatment eggs in those highly used areas. This would coincide with greater densities of jays usually encountered in and around campgrounds, picnic areas and other highly developed areas (Bensen 2008; Suddjian 2009). Loss of treated eggs to bear predation can be minimized by deploying eggs in late winter or very early spring, when bear activity is still at a minimum. To compensate for non-corvid predation still impacting effectiveness of a first deployment, a second deployment could follow several weeks later to ensure complete exposure of all corvids. Revisiting egg locations during a second deployment would also allow assessment of predation rates to facilitate decisions about potential adjustments in deployment methods. Reliable survival estimates of Steller's Jays are not available to date, but annual adult survival rates of 55-65% in the closely related Blue Jay (*Cyanocitta cristata*, Tarvin & Woolfenden 1999) suggest that the slightly larger Steller's Jay may survive equivalently or better. Thus, applications of CTA treatment in every other year may be sufficient and effective in continuously protecting murrelet eggs. Recommendations regarding spatial and temporal treatment intervals are tentative and should be refined in further study. The results of the present study suggest that CTA techniques that are adapted to local circumstances may be a highly efficient emergency management technique to improve murrelet productivity at relatively low cost.

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Appendix – Egg predation as an individual behavioral strategy in Steller’s Jays

A proportion (36%) of the jays captured and subjected to eggs did not recognize, attack and consume eggs as food items. This is a new and significant result with important management implications. Recent research has demonstrated that individual behavioral strategies in Steller’s Jays are stable over time and correlated across contexts. Risk-prone, highly explorative, far-travelling jays that use complex foraging strategies coexist with risk-averse, non-explorative, travel-shy, simple foragers in the same population (Gabriel & Black 2010, Rockwell et al. in press). We quantified the willingness to take risks by jays captured for CTA treatments, and compared their risk-taking tendency to their egg attack behavior during habituation to captivity.

While in captivity, jays were presented with a box trap (Live Animal Two-Door Cage Trap Model 1045; 92 x 25 x 30 cm; Havahart Products) of the same size and build that they were originally captured in. The trap was locked open (it would not close), and baited with peanuts. Jays were monitored for 60 min and their willingness to re-enter the familiar trap was assessed during this period. We assigned behavior scores between 1 and 5 based on distance they were willing to enter into the familiar trap (1: perched on top; 2: at entrance; 3: entered halfway; 4: entered the trap all the way to the bait but stayed less than 2 s; 5: entered all the way to the bait for more than 2 s). We recorded each jay’s initial latency in minutes to perform each of the five behaviors, and assigned a latency of 65 min for the riskiest behaviors not performed during the 60 min observation period. If birds skipped a step and performed a higher-scoring behavior at any time during the experiment, they received a latency of 0 for lower-scoring behaviors that they did not perform. We summed latencies in each of the five behavior scores to obtain an overall cumulative latency for each bird. Birds that did not perform any of the behaviors consequently received a maximum cumulative latency of 325 min, representing a maximally risk-averse individual.

We quantified the willingness to re-enter a familiar trap in 17 jays. 12 of these individuals opened and consumed whole eggs offered in captivity, whereas 5 individuals did not. Jays that consumed whole eggs tended to enter the familiar trap faster than jays that never consumed whole eggs ($t_{15} = 1.90$, $P = 0.077$; Fig. A1). All jays that consumed whole eggs entered the trap

far enough to risk capture (behavior score 4 or 5), whereas only 40% of jays that did not consume eggs did so (Fisher's exact test: $P = 0.015$).

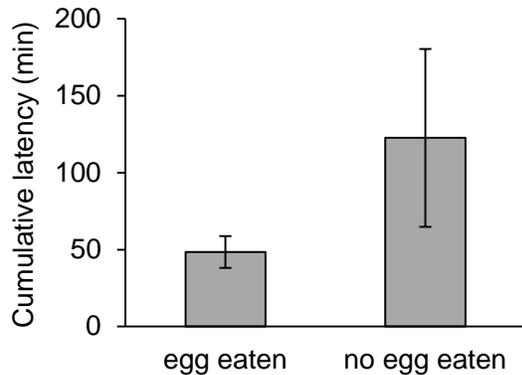


Figure A1. Mean cumulative latency to perform 5 behaviors at a familiar trap (perched on top; at entrance; entered halfway; entered all the way for less than 2 s; entered all the way for more than 2 s) of 12 Steller's Jays that consumed whole eggs and 5 jays that did not consume whole eggs. Error bars denote ± 1 SE.

Although sample sizes for these comparisons were small, this data suggests that egg predation may be part of a range of behavioral specializations in Steller's jays, and not characteristic of all individuals. Risk-prone, highly explorative birds may be more likely to sample rare food sources such as bird eggs. Thus, the predation pressure exerted on murrelet or other avian eggs is probably unevenly distributed across the population of jays. The implication for management actions using CTA techniques is that only jays that pose an actual threat to

other bird eggs will be affected by the CTA treatment. Aversive treatment will automatically be targeted towards egg predators in the population without wasting resources for treatment of individuals that are unlikely to predate bird nests. The implication for lethal management techniques, however, is that unselective removal of resident individuals (without knowledge of their behavior) may exacerbate the predation risk well beyond the influx of non-breeders that is expected after a removal. When a removed individual is eventually replaced by a new breeder, there is risk that the new individual may be more prone to prey on eggs than its removed predecessor. Thus, if lethal removal techniques are considered in extreme situations, it may be prudent to determine the distribution and identity of behavioral strategies. The measure of individual risk-taking behavior used in this study is easy to obtain in wild jays, is correlated to other behavioral strategies (Gabriel & Black 2010, Rockwell et al. in press), and may allow us to make inferences on egg eating behavior of wild jays necessary for precise, targeted management actions.