OBSERVATIONS OF INCUBATION IN YEAR 8 OF A LONG-TERM MONITORING EFFORT AT A MARBLED MURRELET NEST IN NORTHERN CALIFORNIA

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ABSTRACT

Marbled Murrelets (*Brachyramphus marmoratus*) have been endangered in the state of California since 1992 and continue to decline across their range. In recent years this has been primarily due to predation of eggs and young at the nest. Very few studies of murrelets have occurred at their nest due to the difficulty of locating and observing active nests. In northern California, a video camera has been installed at one nest since 2001 and each nesting attempt has been recorded. The 2008 nesting season is reported. In 2008, an egg was laid and survived 29 days before being predated by a Steller's Jay (*Cyanocitta stelleri*). Each morning between egg lay and nest failure, one murrelet departed from the nest 41 min 43 sec±56 sec (x̄ ±SE) following sunrise and the other member of the pair arrived at the nest 41 min 53 sec±66 sec after sunrise. When arrival occurred before departure from the nest, both members of the pair were present at the same time; this co-attendance occurred for a total duration of 2min 2 sec across the entire recorded incubation. Three instances of egg neglect were recorded within the first 9 days of incubation, totaling 24 hrs 11 min 20 sec. While incubating at the nest, murrelets remained motionless (with the exception of blinking) 98.7±1.1% of the time. Murrelets would turn their egg 1.8±5.2 times per hr, primarily using their feet. More egg turns occurred when leaves and branches surrounding the nest-site moved because of the wind. Other behaviors were also recorded including preening, head lifting, and gaping. A rarely reported behavior, described here as feather compression, was also observed regularly and may have been related to the presence of threats near the nest. Considering all nesting attempts at this site, this nest has successfully fledged young 25% of the years. Further, this nest-branch has been used in 6 of 8 years. Finally, at least one member of this breeding pair was a minimum of 9-11 years old.

The Marbled Murrelet (*Brachyramphus marmoratus*) is a small seabird of the family *Alcidae* whose populations have declined over the last 3-5 decades due to anthropogenic activities, including oil spills (Carter and Kuletz 1995), gill net fishing (Carter et al. 1995), and particularly the loss and fragmentation of nesting habitat resulting from the harvest of old-growth coniferous forests (Carter and Erickson 1992, Rodway et al. 1992, Kelson et al. 1995, Perry 1995). In 1992 the Marbled Murrelet (hereafter murrelet) was state-listed as endangered in California (California Fish and Game Commission 1992). Also in 1992, murrelets were federally-listed as threatened in Washington, Oregon and California (U.S. Fish and Wildlife Service 1992). Recent studies have shown that murrelets in California continue to decline (Burger 2002, Strong 2003, Miller et al. 2006, Falxa et al. 2009, U.S. Fish and Wildlife Service 2009). Further, near shore surveys conducted during summer 2008 near Santa Cruz failed to detect juvenile murrelets for the first time, signifying a major contraction of the southern range of the population (Peery et al. 2008, Peery et al. 2009).

Many aspects of the murrelet's nesting ecology and biology remain poorly described. This is because murrelets fly to nests during twilight hours (Nelson and Hammer 1995a), nest in the upper canopy of old-growth conifers (Nelson and Hamer 1995b, Jordan and Hughes 1995, Manley and Kelson 1995, Naslund et al. 1995, Golightly et al. 2008), and their plumage, nest-site, and breeding behaviors are cryptic (Carter and Stein 1995, Nelson and Hammer 1995a). Consequently, nests are rarely found and, once found, remain nearly impossible for investigators to observe for the entire egg incubation period (28 days; Hébert and Golightly 2006). In fact, only 39 murrelet nests have been exactly located in California since discovering that murrelets nest high in old-growth trees (G. Falxa 2010, pers. comm.).

Due to the difficulty of studying murrelets at their nest, many aspects of the murrelet's incubation biology and behavior at the nest have not been described (DeSanto and Nelson 1995, McShane et al. 2004, Hébert and Golightly 2006, Hébert and Golightly 2007, Golightly et al. 2008). Since 2001, one nest in northern California has been continuously observed using remote video recorded throughout each breeding season. Long-term video monitoring has provided an opportunity to make detailed observations of nest failure and daily activity at the nest, as well as assess longterm productivity, longevity, and nest-site fidelity. Herein we describe observations from the 2008 year. Previous years were reported elsewhere (Hébert and Golightly 2006, Hébert and Golightly 2007).

METHODS

This study was conducted at Redwood National and State Parks (hereafter RNSP) in Humboldt County, California. RNSP is one of the largest remaining areas of suitable breeding habitat in California (Ralph et al. 1995, McShane et al. 2004, Hébert and Golightly 2006, U.S. Fish and Wildlife Service 2009, Golightly and Gabriel 2009). In California, murrelets generally nest in stands of old-growth Redwood (*Sequoia sempervirens*), a habitat type unique to this southernmost extent of their range (Hébert and Golightly 2006, Golightly et al. 2009).

In 2001, the right leg of the female bird occupying this nest-site was banded with a metal U.S. Geological Survey band (Figure 1) when she was captured at sea as part of a larger effort to find nests using radio telemetry (Hébert and Golightly 2006). Using telemetry, the nest-site was exactly located in 2001 within RNSP. The nest-tree is an old-growth Redwood located 3.2 km inland from the ocean, with the nest-site located 65.7 m above the ground on a limb that has a 36.0 cm diameter. Vegetation surrounding this nest-site was predominantly Redwood leaves originating from the nest-branch and epiphytic Leather-leaf Ferns (*Polypodium scouleri*; Whitmore and Smith 1993).

Beginning in 2002, the tree was rigged for climbing and a video camera was installed at the nest-site. Each year following, this specific murrelet nest has been monitored using video recordings during the breeding season (mid-March to mid-September; Nelson and Hamer 1995b). To observe the breeding pair in 2008, a persistent, waterproof, varifocal zoom video camera (Model KPC-VF325NH, DSP Color CCD Camera, KT & C Co., Los Angeles, CA) was placed approximately 40 cm from the nest on 9 May. A camouflaged cable wrapped around the tree and lead down to the ground where digital video of all daylight hours was recorded onto an external hard drive. Power was supplied using two Absorbed Glass Mat batteries (Model AGM8A27, East Penn Mfg. Company, Lyons, PA) which were replaced every 3 days. On the ground, computer equipment to manage data storage was cached in a weather-resistant structure 25 m from the base of the tree (Figure 2). Hard drives were exchanged for data retrieval every 3 days. The camera was programmed to begin recording slightly prior to sunrise (0500 PDT) and stop recording after sunset (2100 PDT).

Two observers reviewed videos at playback speeds up to 12 times (12x) faster than normal playback speed, making it possible to completely process 1 hr of video in less than 1 hr. Between nest initiation and nest failure, each video recorded during 0500-0600 hr was reviewed at normal playback speed to observe incubation exchanges. Incubatory exchange was the daily alternation of egg incubation responsibilities where one individual of the pair arrived at the nest and the other departed from the nest. These exchanges occurred approximately every 24 hrs around sunrise (between 0500-0600 hr; Simons 1980, Hirsch et al. 1981, Nelson and Peck 1995, Bradley et al. 2004). For all adult arrivals and departures during incubatory exchanges, time (PDT) relative to official sunrise, and directionality of nest entrance and exit was recorded.

Predatory interactions, egg neglect, and co-attendance potentially occurred at any time of day, and were easily detected through high-speed review of video. Therefore, to detect predatory interactions, egg neglect, and co-attendance, videos recorded during 0600-2100 hr between nest initiation and nest failure were reviewed at 8x normal playback speed. A predatory interaction was any interspecific interaction that led to, or could lead to, nest failure. This included any interaction between the murrelet and another species that caused the incubating murrelet to defend or flush from its nest-site. For each predatory interaction we recorded the species involved, day of the incubation period, and the duration of the interaction. Also recorded was the distance between the murrelet and the other species, which was estimated using the murrelet's culmen length (1.813 cm, n=102; Hèbert and Golightly 2006). Culmen length of the murrelets was used to estimate distance because it could reliably be seen during inter-species interactions, variation in this trait across individuals was small (Hèbert and Golightly 2006), and it was an appropriate length to use based on the camera's field of view (30 cm).

Egg neglect was said to occur when egg incubation was suspended and the egg was left unattended at the nest; however, we excluded of times where the murrelet was forced off of the nest by predatory interactions and times during incubatory exchanges where the egg was briefly alone between departure and arrival. For each instance of egg neglect we recorded the day relative to egg lay, duration of neglect, and gender of adult responsible for neglect. Gender of the individual attending the nest each day was determined by sighting the metal leg band on the female murrelet's right leg coupled with knowledge of a 24 hr cyclical interval between incubatory exchanges for this species.

Co-attendance was defined as when both members of the breeding pair were in attendance at the nest. The time (PDT) of day where adults were in co-attendance at the nest

during incubation was noted. Also, we recorded the frequency and duration that the adult murrelets were in co-attendance at the nest.

To describe and quantify the amount of motion at the nest during incubation, egg turning, and additional adult behaviors while incubating recorded videos were sampled because it was time intensive to review video at normal playback speeds. Motion at the nest during incubation was defined as any time that the murrelet moved, with the exception of the eye blinking. Motion was quantified by systematically sampling 58 hrs of video distributed across the entire incubation using an 8-day rotation such that each hour between 0500-2100 hr was sampled every 8 days. For example, on day 1 hours 5 and 13 were sampled; on day 2 hours 6 and 14 were sampled, and so on until day 9 where hours sampled were the same as day 1. To put into perspective the amount of motion occurring at a murrelet nest, motion at 35 randomly selected Common Murre (*Uria aalge*) nests was quantified using half hour intervals distributed across each nest's incubation period. Common Murre were chosen because they are alcids that share evolutionary history with the murrelet. Further, motion at nests has not been reported in the literature for other avian species (tree or rock-nesting alike) and Common Murre was the most appropriate species as a control because we had access to similar video of murres nesting.

To describe egg turning, we noted the method murrelets used to rotate their eggs and quantified the overall frequency that eggs were turned. A linear regression was used to determine if the frequency of egg turning changed relative to the day of egg incubation, and a t-test was used to determine if eggs were turned at similar frequencies in morning and evening hours. Frequency of egg turns were measured for 50 morning hours (0500-1300 hr) and 50 evening hours (1300-2100 hr). Each hour was randomly selected and each egg turn occurring in selected hours was used for this analysis.

In addition to providing a basic description of egg turning, we asked if the intensity of wind influenced the occurrence of egg turning. To answer this question, 15 hrs of additional video were randomly selected and searched for egg turns. Then wind intensity was described for 10 sec intervals during each egg turn and at 5 min prior to each egg turn. The purpose of describing wind intensity 5 min before the turn was to establish the background wind intensity and provide a comparable expected value for analyses. Wind intensity was measured with a modified version of the Beaufort Wind Force Scale, which was originally created to standardize descriptions of wind intensity using qualitative wind conditions in absence of data on exact wind speed (Oliver 2005). We used movement of leaves and branches to scale wind intensity, ranking wind intensity using a modified 5-point wind scale (Table 1). Chi-squared statistics were used to analyze whether the wind at time of egg turning differed from an expected value derived from 5 min measurement before egg turning.

Additional adult behaviors occurred at the nest during incubating including behaviors that occurred frequently (at least every hour) as well as rare behaviors. We described any behaviors that had not been witnessed by Hébert and Golightly (2006). To observe these additional adult behaviors all video reviewed in normal playback speed was used.

Finally, following nest failure, empty-nest videos were recorded between 0500 hr and 0800 hr each day for 1.5 months post-failure to ensure that any post-failure nest visitations and re-nest attempts could be observed. Video recorded after nest failure was reviewed in entirety at 8x playback speed.

RESULTS

We observed the incubation of one egg for 29 days in 2008. The camera was installed on 9 May and an adult murrelet was present at the onset of the installation process. Approximately

431 hrs of video were recorded over the 29-day egg incubation period (9 May-7 June 2008), with an additional 432 hrs of video recorded post-incubation from 8 June to 24 July. Therefore, we observed the entire nesting attempt, all post-failure nest visitations, potential for re-nesting, and potential predators that landed at the nest.

Chronology

Prior to nest failure, the egg incubated for 29-31 days. The video camera was installed at the nest on either day 0 or day 2 following egg lay. Thus, the egg was laid on either 7 May or 9 May. These dates were inferred by knowing that it is generally the male's responsibility to take the first incubatory shift following egg-lay (Hébert and Golightly 2006) coupled with 29 days of incubation recorded at the nest. Hereafter, we describe the chronology as if egg-lay occurred on the same day as camera installation, but we acknowledge that it is possible that it may have been laid 48 hrs earlier than the reported date.

With the exception of 15 May, an adult arrived at the nest each morning shortly after official sunrise for the incubatory exchange. On 15 May the male murrelet failed to arrive for the incubatory exchange following the female's departure, resulting in a 24 hr bout of egg neglect which ended upon the female's return to the nest for her regular incubation shift.

Steller's Jays (*Cyanositta stelleri*) were first seen near the nest on day 22 of incubation and again on day 27 (Table 2). A jay successfully removed the adult murrelet and predated the egg on day 28; the jay removed the egg from the nest on the day 29. The chick was alive at the time of predation because it could be seen moving inside the egg when the Steller's Jay punctured the egg with its bill on day 28. During the 48 hrs prior to egg removal, one or more Steller's Jays visited the nest 21 times for a total duration of 22 min 44 sec at the nest.

Two hours after egg removal, a Common Raven (*Corvus corax*) landed at the nest and appeared to eat the few remaining egg shell fragments that remained from when the egg shell was initially broken by the jay. Between egg removal on 7 June and when recording was terminated on 24 July, murrelets did not visit the nest-site or attempt to re-nest at this site.

Nest Failure

The egg laid at this nest was killed and then removed by a pair of Steller's Jays on 6 and 7 June, respectively. The first appearance of Steller's Jays in the video occurred on 31 May, 7 days before the egg was killed. During this first visitation, a Steller's Jay was recorded landing within 6 cm of the nest for 12 sec at 0937 hr. Although the jay did not approach the nest directly, the murrelet's reaction to the Jay's presence was immediate; 1 sec prior to the jay arriving in view of the camera the murrelet compressed its feathers to its body. At 0939 hr, 2 min following the initial visitation, two Steller's Jays landed on branches peripheral and parallel to the nest (approximately 3 cm distant), and then left without directly approaching the nest. The jays were detected by the camera for 28 sec during this visit. With the exception of compressing its feathers to its body, the murrelet did not move at all while the jays were near the nest. The murrelet remained motionless for 12 min 12 sec following jay departure.

On 5 June, there were 3 separate jay visitations to the nest, each by a lone Steller's Jay. The first visit occurred at 1326 hr, with a Steller's Jay visible in the camera's field of view for a total duration of 8 sec. The jay landed on a branch immediately above the nest (2 cm distant from the murrelet), hopped in a half-circle around the incubating murrelet, and then departed. In response, the murrelet compressed it feathers and gaped. The feathers were compressed 5 sec prior to the jay entering the camera's field of view and continued for 40 sec following the Jay's departure from view of the camera. Both the second and third visits occurred during the 1800 hr and were similarly short in duration. The presence of a jay was also indirectly detected during

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the 1800 hr, inferred from movement of branches immediately above the nest from a jay-sized bird landing, coupled with observation of the murrelet exhibiting the behaviors of feather compression and gaping at the same time.

On 6 June, one Steller's Jay landed at the nest at 1508 hr and proceeded to physically engage the incubating adult male murrelet by repeatedly circling and provoking the murrelet to lunge in defense 20 times. While turning to face the moving jay, the murrelet gradually moved off the egg until it fell from its position in the tree and out of the view of the camera. The fall occurred 1 min 7 sec after beginning to actively defend the egg from the jay. The Steller's Jay followed the falling male murrelet out of view of the camera. Returning to the nest 20 sec later, the Steller's Jay punctured a hole into the egg using its bill within 11 sec of arrival at the egg. Through the hole the chick could be seen moving. A second Steller's Jay landed at the nest 49 sec after the egg was punctured by the first jay (both in view of the camera). This was likely the mate of the first jay, based on a wing flicking display made by one jay towards the other jay, a behavior most commonly observed in mated pairs as both a courtship begging behavior and an appeasement behavior (Verbeek 1972). The nest was entered and exited by jays 15 times during the evening of 6 June, which totaled 19 min 50 sec of jay presence at the nest. The two jays stuck their bills into the egg 153 times, presumably ingesting aqueous egg contents. On 6 June, the last observation of a Steller's Jay was at 1955 hr and the male murrelet returned to the nest at 2036 hr (41 min 27 sec following the last jay observation). Upon return to the nest, the male murrelet resumed incubation of the punctured egg.

On 7 June, the female murrelet arrived at the nest for her incubation shift at 0512 hr and successfully exchanged positions with the male, sitting upon the punctured egg. Approximately 10 min 37 sec following the incubatory exchange, a single Steller's Jay landed at the nest. Upon landing the jay repeatedly and rapidly circled the nest, provoking the murrelet to lunge repeatedly in defense for 59 sec. One final lunge at the jay caused the murrelet to become precariously positioned at the edge of the branch, and the murrelet departed from the nest-site and was not seen again. Within 1 min of the murrelet's departure from the nest, the Steller's Jay inserted its lower mandible into the hole of the egg and, while grasping the egg, flew away from the nest.

A Common Raven landed at the nest-site 2 hrs after the egg's removal and thoroughly combed through the vegetative materials at the incubation site, appearing to ingest egg shell fragments remaining at the nest. This was the only observation of a Common Raven at the nest during 2008. Following egg removal, murrelets were not recorded returning to the nest for the remainder of the 2008 nesting season.

Murrelet Activity at the Nest during Incubation

Egg Neglect.— During the 2008 breeding season, the egg was left alone by incubating adults on 3 occasions all occurring within 9 days following egg lay (Table 3). The egg was alone for a minimum duration of 24 hrs 11 min 20 sec, or 3.5% of the entire incubation period (we excluded times where it was too dark to visually confirm the start of egg neglect). The male was responsible for 2 instances of egg neglect totaling 24 hrs 07 min 42 sec (99.75%), and the female was responsible for 1 instance of egg neglect totaling 3 min 38 sec (0.25%).

Incubatory Exchange.— One member of the breeding pair flew from the ocean to the nest-tree each morning (excluding 15 May when there was an instance of egg neglect, Table 3) to exchange incubation duties with its mate. The timing and directionality of 25 arrivals to the nest were recorded; however, 4 arrivals were not recorded (3 due to recorder malfunction and 1 due to an occurrence of egg neglect). Additionally, the timing and directionality of 23 nest

departures were recorded. The remaining departures were not recorded due to equipment problems (n=4), an occurrence of egg neglect (n=1), and departure during early lighting conditions (n=1).

Bird arrival at the nest averaged 41 min 53 sec±66 sec ($\bar{x}$ ±SE, n=25 departures) following sunrise. No difference was detected between the male and female in their timing of arrival relative to sunrise from the nest (t_{23}=-1.06, P=0.302), and both murrelets were always recorded entering the tree from the northwest (Figure 3). On 24 occasions a murrelet landed on the branch near the nest-site then walked into the nest. On 1 occasion the adult murrelet dropped into the nest from above and was not visible until it had landed at the nest.

Departure from the nest occurred at an average of 41 min 43 sec±56 sec (n=23 departures) after sunrise. For every departure, the departing bird was observed leaving the tree in a south/southwest direction (Figure 3). For 9 of the departures the murrelet got off of the egg and immediately left the nest-site. For 12 of the departures the murrelet briefly walked around the nest before departure, and on 1 occasion the adult used a branch above the nest as a takeoff platform. The directionality of departure could not be described on 1 occasion due to insufficient light and thus inability to see the murrelet's method of exit.

Co-attendance.— In 2008 co-attendance only occurred during 73.9% of incubatory exchanges. The total duration of co-attendance throughout the 29-day incubation period was 2 min 2 sec (8 sec±2 sec each day, n=15 observations). The remaining 26.1% of incubatory exchanges lacked co-attendance because the departing member of the pair left prior to the arrival of the returning mate. As a result, the egg was alone for 22 min 39 sec throughout incubation (3 min 14 sec±1 min 22 sec each day, n=8 observations). Exchanges lacking co-attendance were not considered egg neglect.

Motion at the Nest.— Although 58 hrs were sampled to determine the proportion of time murrelets spent motionless at the nest during incubation, only 49 hrs could be used; Videos were excluded when there was no murrelet in attendance at the nest (n=5), or when a there was a recording error such that the video was distorted or was not recorded (n=4). Based on the 49 video-hours sampled, murrelets at this nest did not move (with the exception of blinking their eyes) 98.7±1.1% of the time. For comparison, at Common Murre nests observed motion was much greater (t_{34}=10.7, $P\leq 0.000$, Figure 4). On average, murres remained motionless only 66.3±3.0% of the time (n=35 nests) and engaged in activities other than blinking and incubating.

Egg Turning.— Of 95 observed egg turns, murrelets solely used their feet to rotate the egg 84% of the time. Additionally, they used their bill in conjunction with their feet for 15% of egg turns. The remaining 1% of egg turns could not be properly described due to poor lighting conditions at dawn. For all egg turns sampled, the bill was never observed as the sole means of turning the egg.

Egg turning occurred at a frequency of 1.8±5.2 turns per hr (n=100 hrs). We attempted to detect a pattern driving variation in the number of egg turns per hour. Day of incubation was regressed against frequency of egg turning and approached significance, potentially indicating an inverse relationship between egg turning and time into the incubation period (F=3.43, df=1, P=0.07, Figure 5). There was no difference in the rate of egg turning for morning versus evening hours (t_{49}=1.17, P=0.24, 2.1±1.0 turns per hr, 1.6±0.5 turns per hr, respectively).

Egg turning occurred less often than expected when there was no wind-caused motion at the nest-site (χ^2=9.6, df=1, P=0.002, n=27, Figure 6). Additionally, egg turning occurred less often than expected when there was only a small amount of wind-caused motion at the nest (only leaves moved) compared to when there was a greater amount of wind-caused motion

surrounding the nest (small and large branches moved; χ^2=17.5, df=1, *P*=0.00003, n=23, Figure 7). There were no times sampled where wind intensity was so great that adjacent trees could be seen swaying in the wind (no category 4 available).

Additional Adult Behaviors.— Other behaviors occurred in addition to egg neglect, incubatory exchange, and egg turning during egg incubation. Although exact rates were not calculated, behaviors that generally occurred at least once during each hour included bill snapping (when the murrelet opened and closed its mouth repeatedly a few times rapidly), bill ups (pointing its bill skyward), head and body shaking, and responding to unknown stimuli (when the murrelet looked around for reasons that could not be determined). Behaviors that occurred daily, but less frequently than each hour, included preening, moving vegetation (e.g., redwood duff) adjacent to the nest-site, and head lifting (where the murrelet quickly stretched its neck such that its head raised skyward relative to the normal position, held it there, then slowly lowered it such that it returned to the normal incubation posture). Behaviors that only occurred when the Steller's Jay landed within 2 cm of the incubating adult were gaping of the mouth (when the murrelet held its bill open for a minimum of 2 sec) and head bobbing (when the murrelet lunged forward repeatedly and rapidly, especially with its head and neck, while keeping its body over the egg).

We also observed a behavior rarely reported (Nelson 1997); it appeared that the murrelet quickly changed the position of the body feathers such that they were held parallel to the body surface (hereafter called feather compression). Normally feathers were held at a greater angle relative to the body surface during incubation. Feather compression gave the appearance of a smaller, potentially more cryptic bird. This behavior was displayed just prior to the arrival of Steller's Jays at the nest, as well as at other times where a cause could not be determined. This behavior was first noticed after data collection started, and although the exact frequency of occurrence was not measured, this behavior generally varied in frequency such that sometimes it occurred multiple times per hour and sometimes it occurred less frequently than each hour.

DISCUSSION

Nest Failure

Murrelets have evolved with predation, as evidenced by their cryptic morphology and elusive nesting habits. At present, nest predation is currently the most common fatality for murrelet eggs and chicks, so frequent that it prohibits successful recovery of the population (McShane et al. 2004, Golightly and Gabriel 2009, Peery and Henry 2009, U.S. Fish and Wildlife Service 2009). Historically, nest predation could not have compromised murrelet to the same degree, or this species would have gone extinct. Unfortunately, this may no longer be the case and conditions under which murrelets have evolved and managed predation have probably changed. Murrelets are predisposed to nesting along canopy gaps, preferably along waterways, which facilitate access to their nest-site (Nelson 1997, Manley 1999, Burger and Bahn 2004, Zharikov et al. 2006). In recent times, many of the edges that murrelets nest along have transitioned from natural to artificial edges (Marzluff and Neatherlin 2006). Conversely, murrelet nest predators such as Steller's Jays and Common Ravens have increased in density along anthropogenic edges because these edges often co-occur with supplemental foods from fruiting shrubs and anthropogenic sources (Marzluff and Restani 1999, Henske et al. 2001, Raphael et al. 2002, Zharikov et al. 2006, Malt and Lank 2009). This spatial overlap of nesting murrelets with dense predator populations has created a situation where predation of murrelet nests has increased markedly. During a multiple-year radio telemetry study of murrelets nesting in RNSP, Hébert and Golightly (2006) calculated annual nest success rates as low as 3.1% and as high as

9.2%; many failures were ascribed to predation. In the Santa Cruz Mountains, nest failure due to predation was estimated to be about 81% (Peery et al. 2004b).

The nest monitored by this study had an average reproductive success rate of 25%, fledging chicks in 2 of 8 years (2001, 2003; Table 4). In two consecutive years (2006, 2007) no egg-laying occurred, so the actual productivity at the nest could be as high as 33% (2 of 6 possible attempts). Of the four remaining years (2002, 2004, 2005, 2008), the egg was killed by avian predators prior to hatching. In 2005, predation occurred prior to civil dawn (the point which the camera can detect light); as a result, the predatory species could not be identified. For years where the predation event was visible, two species of corvid were identified: Steller's Jay and Common Raven. Steller's Jays have been responsible for 2 egg predations at this nest (2002, 2008) whereas a raven was responsible for 1 egg predation at this nest (2004). Steller's Jays were recorded visiting this nest in both years that nesting did not occur, whereas ravens were not.

Based on video recorded at this one camera-monitored nest, egg predation appears to be the dominant form of nest failure inflicted by nest predators. All nests failures from 2001-2008 occurred during the egg stage. In both nesting attempts where the egg successfully hatched, the resulting chick always survived to fledge. This was true even for the chick in 2003 that was approached within 0.5 m by a Steller's Jay at 1-2 weeks post-hatching (the range resulting from uncertainty about the exact day of hatch due to equipment failure surrounding the day of hatch; Hébert and Golightly 2007). Data collected by Hébert and Golightly (2006) during their radio telemetry investigation showed that chicks are also lost to predation, but to a lesser degree than eggs.

Until recently, it was commonly thought that Steller's Jays were not capable of flushing an incubating murrelet off of its nest (McShane et al. 2004, U.S. Fish and Wildlife Service 2009). This incorrect assumption has led other investigators to conclude that egg predation by corvids was primarily done by Common Ravens, leaving Steller's Jays overlooked as significant contributors to murrelet egg predation. However, jays are unequivocally successful at removing an incubating murrelet from its nest to gain access to the egg.

Our study has significantly enhanced existing knowledge of murrelet nest predators as it provides 3 of 5 (60%) nest-predator identifications that do not depend on inference or assumption. Apart from this study, the literature only cites two additional instances for which nest predators have been identified at non-artificial murrelet nests; one Steller's Jay and one Common Raven (Singer et al. 1991, Nelson and Hamer 1995a, McShane et al. 2004). Because of the cryptic nature of nests located high above the ground, most early attempts at assigning responsibility for predation used association of presence, or simply speculated based on the presumption that jays were incapable of displacing an adult murrelet. Although both corvid species (jays and ravens) contribute to nest predation, a recent investigation of murrelet nest predators using artificial nests reported that Steller's Jay were implicated as being responsible for regional patterns of predation risk (Malt and Lank 2009). Additionally, Steller's Jays are more abundant in forested systems than in the past (see George 2009). Consistent with Malt and Lank (2009), in all years since 2001 Steller's Jays have been observed at the videoed nest, whereas ravens were only seen in 2 of the years. Thus, we conclude that Steller's Jays are likely the primary egg predator at murrelet nests in California and southern Oregon. Many additional avian and mammalian species have been implicated as potential nest predators, but specific evidence at this time does not exist to support contribution by other predators (McShane et al. 2004, U.S. Fish and Wildlife Service 2009).

Reliable and unambiguous identification of murrelet nest predators requires the use of camera technology (Hébert and Golightly 2006, Malt and Lank 2009, Richardson et al. 2009). This non-invasive monitoring method facilitates daily, up-close observations at the nest unlike other methods traditionally used to conduct terrestrial murrelet research (e.g. audio-visual surveys, radar surveys, radio telemetry). The predation event in 2008, from jay arrival to egg puncturing, occurred over a period of 99 sec, or 0.004%, of the recorded incubation period; the chance of actually visually observing a predation without digital record would be very low, even if the nest were at eye level rather than 65 m above ground. Since nest failure is responsible for poor reproduction, and by inference, the continued population decline of murrelets in California, successful recovery will require that management strategies are directed at reducing egg predation (Nelson and Hamer 1995b, McShane et al. 2004, Hébert and Golightly 2006, Golightly and Gabriel 2009, U.S. Fish and Wildlife Service 2009). Because the biology of egg predators differs according to species, accurate identification of murrelet nest predators is very important.

Murrelet Activity at the Nest during Incubation

Egg Neglect.— The occurrence of egg neglect during incubation has not been well-documented for murrelets (Nelson and Hamer 1995b, Nelson and Peck 1995, Hébert and Golightly 2006). Video data at our nest provided evidence that eggs can be left unattended for 24 hrs at a time, and that there was variability in the duration and timing of neglect. However the neglect never exceeded the length of 1 incubation shift, presumably because the second bird arrived to replace the missing incubator. The telemetry study by Hébert and Golightly (2006) reported that 33% of murrelets nesting in RNSP exhibited irregular incubation patterns. Nelson and Peck (1995) observed egg neglect on two occasions at one nest with the longest duration being 4 hrs. Within the auk family, rates of egg neglect tend to be species-specific and are therefore not easily generalized across the family, unlike many other reproductive traits (DeSanto and Nelson 1995). Common Murres and Thick-billed Murres (*Uria lomvia*) generally do not leave their eggs alone (Gaston and Nettleship 1981) whereas Xantus's Murrelet (*Synthliboramphus hypoleucus*) and Ancient Murrelet (*Synthliboramphus antiquus*) leave eggs unattended for multiple days (Murray et al. 1983, Gaston and Powell 1989). The pattern of egg neglect in Cassin's Auklets *(Ptychoramphus aleuticus)* appears similar to what we observed at the murrelet nest in 2008, with egg neglect generally restricted to first half of incubation (Astheimer 1991).

Causes of egg neglect at Marbled Murrelet nests are not understood, but nest disturbance is commonly cited as promoting egg neglect (Winn 1950, Simons 1981, Sealy 1984, Murray et al. 1983, Gaston and Powell 1989). However, we did not consider disturbance-related egg abandonment to be egg neglect since neglect implied a discretionary absence, whereas disturbance-related egg abandonment implied that the murrelet was forced off the egg as a result of immediate need.

The most commonly cited situation that resulted in a non-disturbance egg neglect event was long incubation periods (>1 day) in seabird species nesting far distances from their foraging areas (e.g. *Procellariiformes*; Pefaur 1974, Boersma and Wheelwright 1979, Astheimer 1991). In such situations, long incubation shifts sometimes forced the incubating individual to leave prior to the arrival of the at-sea mate to avoid starvation (Boersma 1982). Murrelets nest within 60 km of the coast (Hull et al. 2001) and forage close to shore (Carter and Sealy 1990, Hébert and Golightly 2006). Additionally, murrelets have relatively short incubation shifts. Thus, foraging pressures and starvation risk are unlikely to be responsible for the 3 instances egg neglect witnessed unless foraging conditions in 2008 were poor, or if foraging itself had been interrupted

on the previous day. Poor foraging conditions for many seabird species have often been associated with low oceanic surface temperatures and an absence of upwelling (Gaston and Jones 1998, Warzybok et al. 2003, Peck et al. 2004, Peery et al. 2006). In 2008, however, the Pacific Decadal Oscillation indices show that surface temperature for the California Current was cooler than average (National Oceanic and Atmospheric Association 2009), implying that fish productivity should have been above average.

Regardless of the cause of egg neglect, these events are significant as they represent times when the egg is exposed at the nest. Although eggs may be cryptically colored, it is unknown if egg neglect facilitates egg predation. Because hatching success is much lower than required for maintaining a stable population growth rate for murrelets in California, an increased understanding of murrelet egg neglect might inform future conservation efforts.

Incubatory Exchange.— Although murrelets have been detected inland throughout the year (Naslund 1993), inland flights occurred much more frequently during incubation and chick-rearing stages of breeding (O'Donnell et al. 1995, Peery et al. 2004a). These inland flights have consequences for management as they represent times when adult murrelets are at risk of mortality from both avian predators (e.g. Peregrine Falcon, *Falco peregrines*; Red-shouldered Hawk, *Buteo lineatus*; McShane et al. 2004, Peery et al. 2006) and human activities along their flight pathways (e.g. encountering on-shore wind-energy projects; U.S. Fish and Wildlife Service 2009). Although the murrelet population has been characterized by low annual reproduction and low juvenile survival, the adult survival must be adequate to maintain the population (McShane et al. 2004, Peery and Henry 2009).

Murrelets fly inland at dawn, beginning approximately 50 min before sunrise and continuing for 70 min after sunrise. (Naslund and O'Donnell 1995, Hébert and Golightly 2006). Fly-in times for the murrelet pair monitored in RNSP fell within that range of time, consistently arriving at the nest 42 min following official sunrise. Because pair-specific observations could be made by our study, we were able to quantify daily variation in flights inland for the nesting pair of murrelets. The consistency of timing of arrival and departure from this nest throughout the duration of incubation was remarkable; on any given day arrival and departure from this nest was highly coordinated in time, and from day to day incubatory exchange occurred at approximately the same time relative to sunrise. We conclude that nesting birds are probably flying directly to the nest and do so without distractions that would cause variation in timing. Additionally, this highly coordinated exchange of breeding murrelets likely evolved due to selection pressures imposed by predation. Raptor species have been known to kill inland flying murrelets; however they are diurnal hunters whose eyes have not evolved for low-light hunting conditions (Ferguson-Lees and Christie 2001, Peery et al. 2004b, U.S. Fish and Wildlife Service 2009).

Directionality of arrival and departure from our nest were also remarkably consistent. This would imply that certain characters of the nest-site dictate arrival and departure pathways. We could not identify exactly what characters dictate arrival and departure paths because this was not explicitly planned for our study. It has been speculated that the high wing-loading characteristic of murrelet morphology may affect maneuverability while flying within the forest canopy, potentially increasing the risk of fatal collision or grounding where subsequent take-off would be difficult (Bradley 2002, Burger 2002). Murrelets could reduce their risk of collision by nesting near canopy gaps, or on sloped terrain, if this allowed departures in relatively open areas of the forest (Bradley 2002, Baker et al. 2006, Zharikov et al. 2006). Conversely, arrivals may require canopy openings conducive to approach and landing. Thus, individual tree-canopy configuration may dictate the landing location (Nelson 1997, Burger and Bahn 2004) and

constrain availability of nest-sites. Furthermore, murrelets are reported to fly to and from nests along consistent flight paths (Nelson and Peck 1995).

Co-attendance at the Nest.— This is the first report to describe co-attendance at a murrelet nest through the entire duration of incubation. Co-attendance occurred during 0.01% of the entire recorded incubation at this nest. Previous descriptions of co-attendance at murrelet nests report a similar duration of overlap at the nest (26 sec) occurring during incubatory exchanges (Nelson and Hamer 1995b, Nelson and Peck 1995). However, beyond these descriptive observations, co-attendance has not been the focus of study for murrelets.

For murrelets, co-attendance at the nest might increase the potential for predation on adults, by flying to and from the ocean when raptor species could be active. It could also increase risk to young, by making the nest-site more visible to predators. Although two murrelets may be more successful than one at defending their egg from a predator, the presence of two murrelets at the nest may greatly increase the probability of detection by predators. If murrelets cannot defend their young once the nest has been discovered by a predator, then successful nests would rely on the concealment of their nest when eggs and chicks were present. If co-attendance increased the probability of nest predation for murrelets, then it should be selected against and occurrence should be limited in duration.

Unlike other seabirds, co-attendance by murrelets is not driven by food availability because co-attendance only occurs briefly during a few incubation exchanges. When co-attendance in seabirds is influenced by food availability, the duration of co-attendance is more variable that what was seen at this murrelet nest. For example, co-attendance at Common Murre nests is used as an indicator of food availability during chick-rearing (Birkhead and Nettleship 1984, Uttley et al. 1994, Zador and Piatt 1999, Parker 2005, Eigner 2009) because it is variable in duration, occurs during incubation and chick-rearing, and is related to the effort to find food (Parker 2005, Eigner 2008). In years with poor foraging conditions co-attendance for nesting Common Murre can be as low as 2.4% (Uttley et al. 1994) and in years with abundant food supply co-attendance has been observed to be as high as 41% (Eigner 2009). Alternatively, if predation risk to flying adults increases with ambient light and flights are avoided during times of good light, a graded response to food available at sea would not be expected.

Motion at the Nest.— This is the first report to describe the amount of motion at a murrelet nest during the entire duration of incubation. While incubating the murrelet was motionless, with the exception of blinking, most of the time. Similar findings were reported by Nelson and Hamer (1995b), who observed 4 nests that were motionless at least 90% of the time. Compared to their murre counterparts, murrelets do not move while at their nest. Because murrelets have fidelity to nest-sites, it is possible that reducing movement at the nest has become an advantageous behavior resulting from recent increases in predation risk by corvids in old-growth habitats (Malt and Lank 2009, Lima 2009, Peery and Henry 2009). It could also be that remaining motionless has evolved in response to long-term predation pressures at murrelet nests, which would be consistent with the cryptic characteristics of nesting murrelets, including their plumage.

Egg Turning.— Egg turning is poorly described for all alcid species. Video recorded at this one nest showed that Marbled Murrelets primarily rely on their feet for egg turning, only rarely using their bill for assistance. This is interesting since most avian taxa studied, including Common Murre (S.R. Schneider, pers. obs.), primarily use their bill for egg turning (Deeming 2002). Deeming (2002) explicitly stated that the role of feet in egg turning was poorly understood and that use of feet may allow for eggs to be turned without rising from the nest. We

speculate that using feet for egg turning confers increased nest concealment, assuming that it allows the egg to be turned with less overall body movement. We also speculate that increased motion at the nest may increase its visibility to potential nest predators because the incubating murrelet remained motionless at the nest between egg turning events.

This study provides the first report of egg turning frequency for murrelets. There was a large amount of variability in the frequency of egg turning throughout incubation. However, neither time of day nor day of incubation accounted for the variation in turning frequency seen at this nest. Wind intensity, however, was correlated with the frequency of egg turning at this one murrelet nest. Perhaps turning the egg during wind gusts ensured that the most prominent movement at the tree was not at the nest, and therefore the potential for predatory species to detect the nest-site using visual cues was diminished. Like other cryptically colored animals, concealment should be accomplished by remaining stationary on a background that is similarly colored; conversely, when murrelets move relative to a stationary background they could be more easily detected (Mizutani et al. 2003, Shohet et al. 2006, Watanabe and Yano 2009). In leaf-mimicking mantids, it was found that they would remain motionless when there was no wind; however as wind velocity increased, mantids would begin to walk and sway in search of prey (Watanabe and Yano 2009). This strategy of moving while wind moves surrounding vegetation was hypothesized to be an effective anti-predator defense as it diminished the ability of predatory species to detect the mantid as it moved (Watanabe and Yano 2009). Watanabe and Yano (2009) provide the only example of an animal exploiting wind-caused motion as a way to remain camouflaged through action. We hypothesize that avoidance of detection by potential predators is also why murrelets are more likely to turn eggs while there is sufficient wind-caused motion surrounding the nest.

Thermoregulation is another possibility that may explain why the egg was turned during wind more frequently; however, this strategy as a mechanism of egg cooling has not been noted elsewhere. The climate of coastal forests in the Pacific Northwest is mild, with average ambient temperatures during the summer remaining between 14.1-17.6^{o}C (Eureka, Ca; Woodley Island Weather Station, 1970-2001 average; National Oceanic and Atmospheric Association 2010). In a study of Crowned Plovers nesting in the hot desert of Kenya, no relationship was found between wind speed and egg temperature for exposed eggs (Brown and Downs 2002). This suggests that ambient temperature, and not wind, has the greatest effect on egg temperature. Furthermore, in a study of three species of passerine nesting in shortgrass-prairie habitats, where the solar radiation was relatively great compared to coastal forests of the pacific northwest, it was found that nests were effective wind barriers, reducing wind velocities by an order of magnitude relative to ambient wind velocity (With and Webb 1993). This suggests that even in relatively hot climates nests may act to break the wind.

Additional Adult Behaviors.— Recognition of behaviors typical of an incubating murrelet may be useful in the future for researchers using video to identify disturbances at the nest (see Hébert and Golightly 2006). An understanding of murrelet behaviors may provide clues to events occurring in the vicinity of the nest that are not visible within a camera's field of view, such as another species closely approaching the nest. Further, use of video technology to monitor nests during chick-rearing would be valuable as it could provide information about chick diet and provisioning rates (Lewis et al. 2004, Parker 2005, Eigner 2009).

Feather compression not noticed in previous years at this nest, probably due to the lower quality of video recordings prior to 2008. This behavior seems similar to a behavior described by Nelson (1997) where murrelets flatten themselves on a tree branch in response to the call or

presence of a predator. Feather compression was witnessed every time a Steller's Jay was visible, and also occurred at times when we could not determine if the murrelet was responding the presence of predatory species nearby. Additionally, the physiological mechanism controlling this morphological expression is unclear. This behavior could be facilitated solely by the erection and compression of feathers (Morris 1956) or air sacks associated with the bird's respiratory system may also be involved (Casler 1973, Wedel 2003). More observations of this behavior will elucidate the true function of feather compression.

Longevity and Nest Site Fidelity

Longevity remains unknown for murrelets, and despite long-term monitoring at this nest it could not be directly measured. Other species in the auk family have been documented to live for a range of 5-32 years (Clapp et al. 1982, DeSanto and Nelson 1995). The only longevity report existing for murrelets comes from the recapture of 2 banded individuals at a minimum age of 7 years (Cooke 1999). However, the nest monitored by our study does provide a third record of minimum murrelet longevity. In 2003 and 2008, the band on the female murrelet was re-sighted (Figure 1). Banded in 2001, the female was a breeding adult. Although age of sexual maturity is not known for murrelets, it is commonly assumed to occur between the ages of 2 and 4 generalizing from the life history characteristics of other alcids (DeSanto and Nelson 1995). This would suggest that, depending on age of sexual maturity, the female murrelet at our nest was a minimum of 9 to 11 years of age in 2008.

Nest-site fidelity is common among both ground (e.g. Common Murre, *Uria aalge*; Birkhead 1977) and burrow nesting alcids (e.g. Razorbill, *Alca torda*, Harris and Wanless 1995; Black Guillemot, *Cepphus grylle*, Ewins 1989). Nest-site fidelity is a common life history trait in alcids and it is not surprising that tree-nesting murrelets could return to the same nest-site in multiple years. Murrelets have been reported to exhibit fidelity to the same nest-stand (Divoky and Horton 1995) and to a lesser extent a specific nest-tree (Nelson and Peck 1995, Naslund et al. 1995). Moreover, our nest monitored in RNSP provides unequivocal evidence that an individual murrelet can exhibit fidelity to both a nest-branch and a nest-site for multiple consecutive years (Figure 8; Hébert and Golightly 2006, Golightly et al. 2008).

All previous breeding attempts recorded at the nest monitored in RNSP were presumed to have included at least one member of the original pair since monitoring began in 2001 (Hébert and Golightly 2006, Golightly et al. 2008). We assumed this because of band re-sightings in 2003, and again in 2008. All nests initiated on this branch, regardless of their exact position, were adjacent to a small patch of vegetative cover growing on the branch.

Although it has been shown that murrelets exhibit fidelity to a nest-site, the duration that fidelity to one site is maintained is not known (Golightly et al. 2008). For the last 6 of 8 years, the murrelet pair studied has nested on the same branch. Four consecutive breeding attempts (2001-2005) occurred in the same exact location on the nest-branch. In 2008, following a two year period where no nesting was observed at this site (2006, 2007), the pair returned to nest; the egg was laid on the same branch 38 cm southeast of the original nest-site used in 2001-2005 (Figure 8).

It is unknown why there was a shift in the precise area of the branch being used for nesting. However, the 38 cm movement implied that one nest-branch may have multiple potential nest-sites. For Common Murre, pairs observed changing nest-site moved less than 2 m from their previous site (Harris et al. 1995). Additionally, it is not understood why a nest-site used by a murrelet pair for multiple consecutive years would become inactive for a period of two years, with re-use resuming in the third year (Golightly et al. 2008). Although there is very

limited understanding of nest-site fidelity in murrelets, it has been suggested that nest re-use would be less common where either nest predation was frequent or where nesting habitat was not limited (McShane et al. 2004).

Previously, the 2-year interruption in nesting at our nest-site was attributed to multiple years of nest failure due to predation (Golightly et al. 2008). Risk of predation is the most commonly documented cause of nest abandonment in birds (Lima 2009), and for Common Murre, nest-sites are commonly abandoned following failed breeding attempts (Hedgren 1980, Harris et al. 1995). If nest-site selection for murrelets was directly influenced by nest failure and predation at a specific site, one would predict that nesting should have halted on this branch in 2003 following the nest failure in 2002, and again in 2005 following failure in 2004. However, this was not the case. Additionally, because breeding resumed in 2008 on the same branch, this could lend support to the hypothesis that fidelity to a nest-site is more influenced by the availability of suitable nest-sites relative to the risk of predation. As the murrelet population declines, breeding habitat should become relatively more abundant since most critical habitat for murrelets is currently afforded protection (U.S. Fish and Wildlife Service 2009, Golightly and Gabriel 2009). Increased availability of nest-branches would potentially allow breeding pairs to choose between multiple nest-sites for each breeding attempt. If this was the case, the murrelet pair monitored at RNSP may have nested at an alternate location in 2006 and 2007 but beyond the camera's view.

Alternative explanations for a suspension in breeding could also include the possible death of the male murrelet between 2005 and 2006. Nest-site fidelity is generally more common when both members of a pair survive to the next breeding attempt (Coulson and Thomas 1983, Aebischer et al. 1995). For our nest, the female has survived for the duration of monitoring. However, it was not possible to confirm that the male participating in the 2008 nest was the same or a different individual than the male(s) seen at this nest in previous years.

Another explanation for the observed pause in nesting is that murrelets do not necessarily breed on an annual basis. In general, members of the auk family tend to lay 1 clutch each year (DeSanto and Nelson 1995). For murrelets, however, initiating nests annually may or may not be common. Hébert and Golightly (2006) and Peery and Henry (2009) report variability in the proportion of the population participating in breeding each year. Decreased breeding effort in murrelets has also been detected in years with low prey availability (Peery et al. 2004a). Additionally, Steller's Eiders (*Polystica stelleri*) and Dark-bellied Brant (*Branta bernicla bernicla*), two species of arctic waterfowl, forgo annual nest initiation in response to predation risk (Quakenbush et al. 2004, Spaans et al. 2006, Lima 2009). Thus it is unknown whether a nest was undetected in 2006 and 2007, or if nesting did not occur as a result of predation or ocean condition.

ACKNOWLEDGEMENTS

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Figure 1. A photo of the female Marbled Murrelet with an arrow pointing to the metal
identification band on her right leg, recorded at the nest in 2008. This murrelet was
originally banded in 2001 during a radio-telemetry study (2001-2003) conducted at
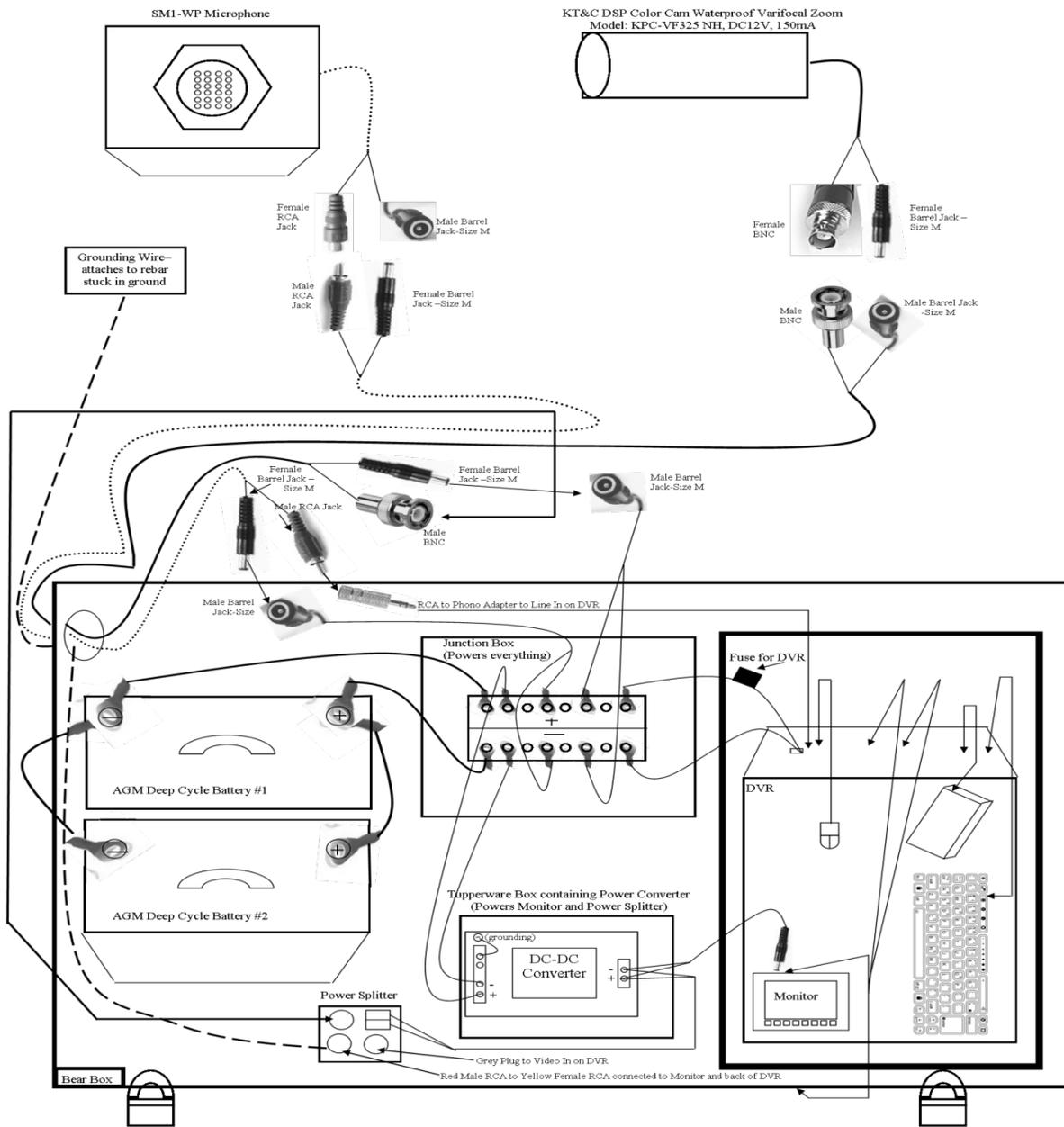Redwood National and State Parks, California.

Figure 2. A diagram of the Digital Video Recording (DVR) system used to monitor the Marbled Murrelet nest in Redwood National and State Parks in 2008. This device was placed in the field and used to record and store continuous video footage of the nest during nesting season. The microphone was not added to the DVR system until the 2009 field season, however it is illustrated because this image was created following the addition of a microphone.

Figure 3. North-oriented Marbled Murrelet nest-site photo highlighting the arrival and departure pathways used by the Marbled Murrelet pair during the incubatory exchange in Redwood National and State Parks in 2008. Arrival at the nest was always from the northwest, following the path of the arrow leading from the landing platform to the 2008 nest-site. Departures from the nest always occurred in a southeasterly direction following the path of the arrow leading away from the nest-site.
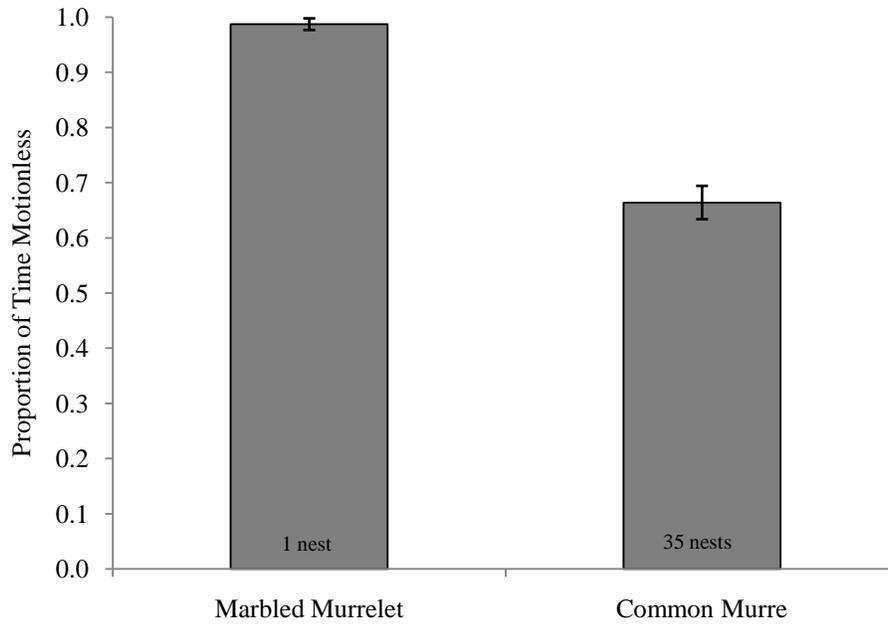
Figure 4. The proportion of time spent motionless (blinking only) while at the nest during incubation by an adult Marbled Murrelet in Redwood National and State Parks in 2008. This is compared to proportion of time that Common Murres spent motionless while at the nest during incubation to put into perspective the amount of motion that occurred at the murrelet nest. Error bars represent standard error.

Figure 5. Egg turning frequency (egg turns per hour) relative to the day of incubation at one Marbled Murrelet nest in Redwood National and State Parks in 2008. The results of the regression analysis approached significance (P=0.07).
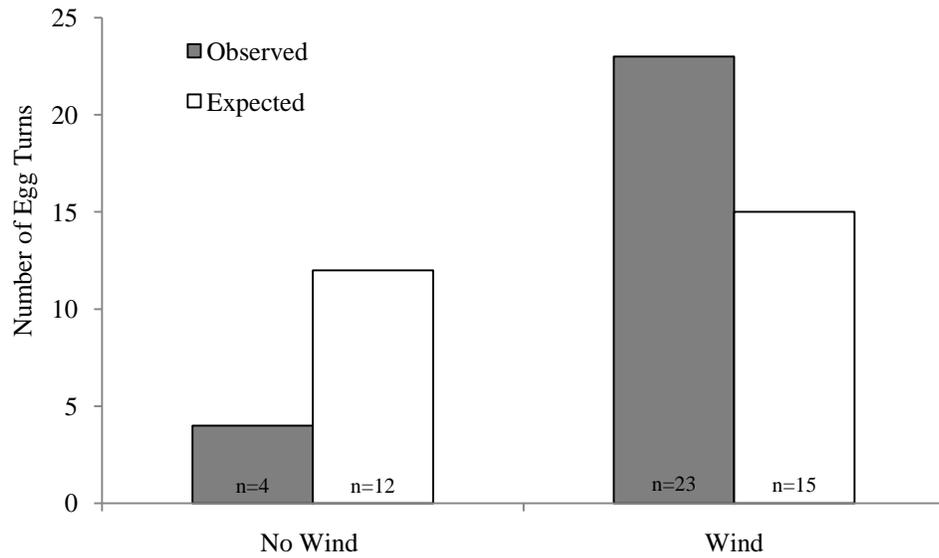
Figure 6. The egg was turned more frequently than expected when there was wind-caused motion surrounding the nest at the Marbled Murrelet nest monitored in Redwood National and State Parks in 2008. Sample sizes represent the number of egg turns for each category.
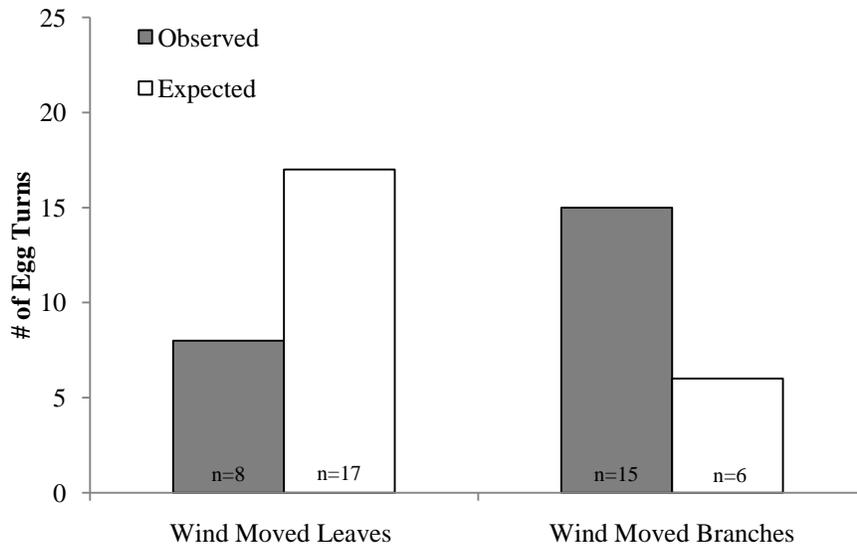
Figure 7. The egg was turned more frequently than expected when the wind was strong enough to move branches surrounding the nest relative to when the wind was only able to move leaves surrounding the nest at the Marbled Murrelet nest monitored in Redwood National and State Parks in 2008. Sample sizes represent the number of egg turns for each category.
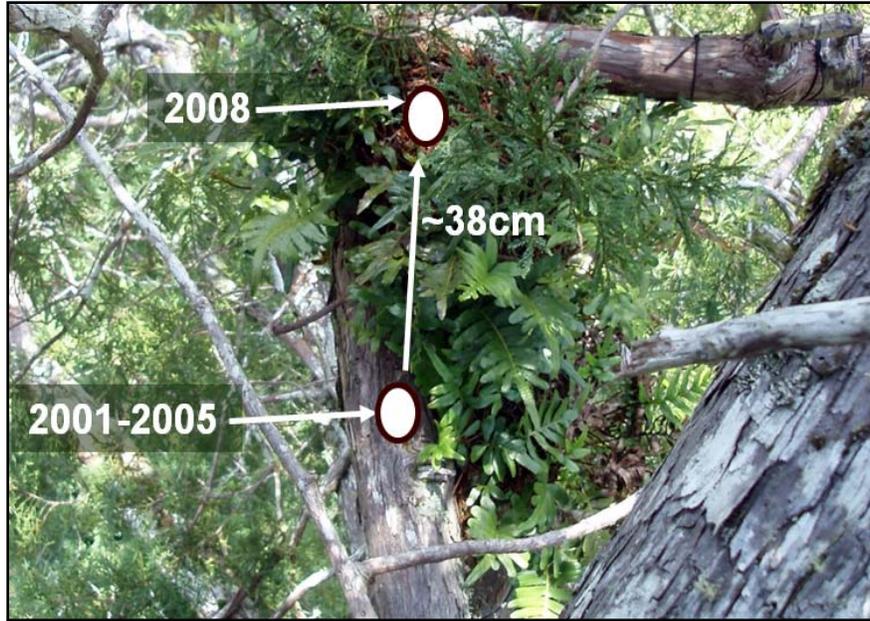
Figure 8. Exact nest-site location for all documented nesting attempts (2001-2005, 2008) on the monitored nest-branch at Redwood National and State Parks, Orick, California. The position of the nest-site in 2008 had shifted 38cm from the nest-site used in 2001-2005. In 2006-2007 there was no documented nesting on this branch.

Table 1. Modified wind scale used to classify wind intensity at the Marbled Murrelet nest
monitored in 2008 at Redwood National and State Parks, Orick, California.

Wind Level	Qualitative Description
0	No wind-caused movement seen at nest
1	Wind-caused movement of leaves surrounding the nest
2	Wind-caused movement of small branches and leaves surrounding the nest
3	Wind-caused movement of large branches surrounding the nest
4	Wind-caused movement of trees surrounding the nest

Table 2. Summary of all Steller's Jay (STJA) activity at one Marbled Murrelet (MAMU) nest during 2008 at Redwood National and State Parks, Orick, California. STJA is an abbreviation for Steller's Jay and MAMU is an abbreviation for Marbled Murrelet.

Days After Egg Lay	Date	Duration Present (mm:ss)	# STJA	Description of STJA Activity
22	31-May	00:01	1	STJA flew beyond nest tree
		02:51	2	STJA landed on branch behind nest
27	5-Jun	00:08	1	STJA flew around nest, did not land
		00:01	1	STJA (not visible) perched on branch above nest
		00:01	1	STJA flew behind nest, landed on branch above nest
28	6-Jun	01:07	1	STJA landed on branch above nest, displaced MAMU
		00:57	1	STJA returned to egg, punctured egg
		00:59	2	Second STJA arrived at nest
		00:38	1	STJA drank egg fluid
		00:09	2	Second STJA arrived at nest, first STJA left
		01:14	1	Second STJA drank egg fluid
		00:18	1	STJA drank egg fluid
		00:22	1	STJA drank egg fluid
		02:09	1	STJA drank egg fluid
		02:12	1	STJA drank egg fluid
		02:13	1	STJA drank egg fluid
		01:54	1	STJA drank egg fluid
		01:46	1	STJA drank egg fluid
		01:53	1	STJA drank egg fluid
		01:36	1	STJA drank egg fluid
		01:30	1	STJA drank egg fluid
29	7-Jun	00:59	1	STJA landed next to nest, displaced MAMU
		00:38	1	STJA grasped egg with bill, flew away
		00:07	1	STJA briefly perched at nest
		00:05	1	STJA briefly perched at nest

Table 3. Instances of egg neglect at the Marbled Murrelet nest during 2008 at Redwood National and State Parks, Orick, California. The following terms are abbreviated: incubation (Incub.) and incubation exchange (IE).

Event	Date	Day of Incub.	Gender	Description
1	12 May	3	Female	Female left prior to dawn, returned to nest before IE
2	15-16 May	6	Male	Male didn't arrive at nest following departure of female
3	7 May	8	Male	Male left prior to dawn, returned to nest before IE

Table 4. Summary of documented nest fates (2001-2008) for the Marbled Murrelet nest monitored at Redwood National and State Parks, Orick, California. Years 2001-2005 were also reported in Hébert and Golightly (2006) and Hébert and Golightly (2007). The species listed in parenthesis next to the cause of failure is the species responsible for the predation event.

Year	Nest Fate	Cause of Failure
2001	Chick Fledged (26 June)	-
2002	Failed at Egg Stage	Predation (Steller's Jay)
2003	Chick Fledged (4 July)	-
2004	Failed at Egg Stage	Predation (Common Raven)
2005	Failed at Egg Stage	Predation (Unknown)
2006	No Nesting	-
2007	No Nesting	-
2008	Failed at Egg Stage	Predation (Steller's Jay)