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The Nesting Ecology of Woodpeckers in the Eastern Cascades and Their Interactions with Nest Competitors and Predators

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THE NESTING ECOLOGY OF WOODPECKERS IN THE EASTERN CASCADES AND THEIR INTERACTIONS WITH NEST COMPETITORS AND PREDATORS.

by

Samuel D. Cowell

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ABSTRACT

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by

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Major Professor: Dr. Kimberly A. Sullivan
Department: Biology

Woodpeckers serve as the primary cavity excavators (PCEs) in temperate forest ecosystems, with secondary cavity users (SCUs) dependent on these cavities for their own nesting success. This creates dynamic nest webs within a community as PCEs excavate nests and SCUs compete for these nests. Here, through the use of continuous video monitoring, we document direct behavioral interactions at the nests of four PCE species and SCUs in the Eastern Washington Cascades during the 2015 and 2016 breeding seasons and how they influence nest web dynamics. Additionally, we offered 937 students in a General Biology laboratory course to participate in this original research opportunity and described the impact the experience had on the participants as well as the researchers.

In 2015, Western Blubebirds usurped two active Black-backed Woodpecker nests by cooperatively harassing the woodpeckesr and guarding the nest. In 2016, almost half of the PCE nests we monitored we reused within the same season by four species of

SCUs, with Western Bluebirds being are most common SCU. We found that some nests we reused within minutes to hours of vacancy by PCEs. However, we were not able to significantly predict nest reuse or SCU presence at the nest. Parent PCEs did not respond as aggressively to avian SCUs when compared to rodent SCUs, predators, and other PCE species. Our fine-scale analysis provides a new window into behavioral interactions in the nest webs and same-season nest reuse, but it is limited by its scope. Thus, we suggest for larger-scale video studies examining behavioral interactions around the nest and how it affects nest reuse within season.

About 15% of students in the course participated in our research, and we found that students accurately recorded data approximately 90% of the time. Most students came away from the experience with a more positive attitude towards undergraduate research and were able to restate the main research question. However, many students had difficulty understanding their role as a data collector. We suggest making the experience mandatory to include all students and placing a greater emphasis on the process of science.

(91 Pages)

PUBLIC ABSTRACT

The Nesting Ecology of Woodpeckers in The Eastern Cascades and Their Interactions with Nest Competitors and Predators

Samuel D. Cowell

Woodpeckers create nesting cavities for other birds and animals in forests. This creates dynamic interactions between both woodpeckers and these other animals. Using video cameras, we documented direct behavioral interactions between nesting woodpeckers and other animals in the Eastern Washington Cascades during the 2015 and 2016 breeding seasons. Additionally, we offered 937 students in a General Biology laboratory course to participate in this original research opportunity and described and the impact the experience had on the participants as well as the researchers.

In 2015, Western Blubebirds took over two active Black-backed Woodpecker nests by physically attacking the woodpeckers. In 2016, almost half of the woodpecker nests were reused by other animals, with Western Bluebirds being are most common SCU. We found that some nests we reused within minutes to hours of vacancy. However, we were not able to significantly predict nest reuse or the presence of other animals at the nest. Parent woodpeckers towards avian cavity nesters when compared to rodent, predators, and other woodpeckers. Our fine-scale analysis provides a new window into behavioral interactions at woodpecker nests and same-season nest reuse, but it is limited by its scope. Thus, we suggest for larger-scale video studies examining behavioral interactions around the nest.

About 15% of students in the course participated in our research, and we found that students accurately recorded data approximately 90% of the time. Most students came away from the experience with a more positive attitude towards undergraduate research and were able to restate the main research question. However, many students had difficulty understanding their role as a data collector. We suggest making the experience mandatory to include all students and placing a greater emphasis on the process of science.

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This research was funded by a joint venture agreement between the U.S. Forest Service and Utah State University, agreement 15-JV-11261992-059. All aspects involving wildlife followed guidelines of the university's institutional animal care and use committee, approval number 2590, and all aspects involving using undergraduate questionnaires for research followed guidelines of the university's internal review board, protocol #7767.

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Sammy

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CHAPTER I

TAG-TEAM TAKEOVER: USURPATION OF WOODPECKER NESTS BY WESTERN BLUEBIRD

ABSTRACT: Woodpeckers provide important ecological services by excavating nesting cavities that are used by many forest birds and other animals. Demand for nesting cavities by secondary cavity nesters can lead to intense competition for this limited resource. The Western Bluebird (*Sialia mexicana*) is known to usurp nests from its own and other species. However, the process by which bluebirds take over nests from woodpeckers larger than themselves has not been well documented. In order to understand this process, we analyzed 112 hours of video footage of nests of a Black-backed (*Picoides arcticus*) and a Hairy Woodpecker (*P. villosus*) located in the Okanogan-Wenatchee National Forest in Washington. Usurpation first involves a short period of physical confrontation followed by a prolonged period of constant presence around the nest. The male and female bluebirds cooperate by taking turns harassing the woodpecker and guarding the nest. This may be of concern to managers as the Black-backed Woodpecker is considered a species at risk in certain locations

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In temperate forests, woodpeckers are the primary excavators of nesting cavities that are later used by many species of birds and mammals. The demand for these cavities by secondary cavity users can lead to intense competition (Miller 2010). Because of this, woodpeckers may be prone to having their nests usurped by both other woodpecker species and secondary cavity nesters (Loeb and Hooper 1997, Kronland 2007). The bluebirds are secondary cavity nesters that defend their own nests aggressively and usurp cavities from other birds (Frye and Rogers 2004, Guinan et al. 2008, Gowaty and Plissner 2015), including woodpeckers (Nappi and Drapeau 2009, Kozma and Kroll 2012). However, these events seem rare (only one event was reported in in the latter two studies), and the mechanism by which bluebirds usurp a woodpecker nest has not been well documented.

Here, we describe the process by which Western Bluebirds (*Sialia mexicana*) usurped active nests from woodpeckers. Our work took place on the east slope of the Cascade Range of Washington. Common primary excavators in this area include the Hairy Woodpecker (*Picoides villosus*), Black-backed Woodpecker (*P. arcticus*), White-headed Woodpecker (*Picoides albolarvatus*), and Northern Flicker (*Colaptes auratus*) (Haggard and Gaines 2001). Both the Black-backed and White-headed Woodpeckers have been petitioned or listed as endangered, threatened, or species of concern in several states and at the national level (Murphy and Lehnhausen 1998, Bonnot et al. 2008). Common secondary cavity users that may compete for cavities are the Western Bluebird, Mountain Bluebird (*Sialia currucoides*), and House Wren (*Troglodytes aedon*) (Haggard and Gaines 2001).

Video cameras recorded active woodpecker nests, and, in reviewing these videos, we observed two usurpations by pairs of Western Bluebirds. We then scored the videos to examine the behaviors by which the bluebirds usurped the nests, nest defense by the woodpeckers, and the progress of the takeover.

METHODS

In 2015 we set up video cameras near woodpecker nests to test techniques for documenting nest failures. Nests were located in burned coniferous forest in the Naches Ranger District, Okanogan-Wenatchee National Forest in Washington state (approximately 46º 45′ N, 120º 58′ W and 47º 30′ N, 120º 33′ W). The fires had been prescribed by the U.S. Forest Service from 2006 to 2014. Their severities were mixed, creating a mosaic of small patches (0.1–24.2 ha), some burned severely (~80–90% canopy mortality), others lightly (~0–10% canopy mortality), in an otherwise live forest. Forest composition varied by aspect, elevation, and distance from the Cascade crest, but most sites were dominated by a mixture of ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotsuga menziesii*), and grand fir (*Abies grandis*).

In total, we monitored over 40 nests of four species, the Black-backed Woodpecker, White-headed Woodpecker, Hairy Woodpecker, and Northern Flicker. We began monitoring our earliest nest on 28 April 2015 and concluded monitoring our latest on 28 June 2015. In this pilot study, the time over which we monitored each nest varied, from two to seven days per week through the season. We used Panasonic camcorders (model HC-V160) with LiPolymer batteries (model 1055275-2C) manufactured by Mogen Industrial Limited. Cameras were mounted on a tree 20–50 m from the nesting cavity. Camera batteries and the 64-gigabyte Secure Digital card were changed out every day.

Of the two woodpecker nests taken over by Western Bluebirds, one (Angel Burn) was an active Black-backed Woodpecker nest. The other (Hause Creek) was originally excavated by Black-backed Woodpeckers, but Hairy Woodpeckers had occupied the cavity by the time filming began. We monitored the Angel Burn nest in the Rattlesnake Creek drainage for six 24-hour periods, on 14 15, 19, 20, 28, and 30 May, the Hause Creek nest in the Tieton River drainage for ten 24-hour periods, 28 April–8 May, skipping 3 May.

Our review of the video recordings began with an initial screening of 2-hour segments in which one of six observers recorded any activity near the woodpecker nest and the time of the occurrence. Observers watched and listened for woodpeckers, Western Bluebirds, rodents, and any other animals that approached the nest. For each animal, the observers recorded the species, sex, behavior, method of detection (visual or auditory), time at which it appeared in the frame, time at which it appeared at the cavity (if applicable), time at which it exited the frame, duration of the event, and if it was alone or interacting with other animals. By these methods, we identified the time from when bluebirds first appeared around the woodpecker nest to when usurpation was complete (defined by woodpeckers not being seen or heard at or around the nesting cavity for at least 24 hours).

Multiple observers then watched all video segments with woodpecker–bluebird interactions a second time and scored them according to an ethogram developed for this study and based on behavior described by Brawn (1984), Guinan et al. (2008), and

Kronland (2007). Interactions were categorized into two categories (displacement or chasing) with two sub-categories (with or without physical contact). Displacement was defined as one bird leaving a spot because of the presence of another bird. Chasing was defined as one bird continuing to aggressively pursue another bird even after the latter already left its previously occupied spot. Any vocalizations or drumming were also scored. For each event, we defined the actor as the initiator of the interaction and the recipient as the one experiencing the initiator's action. We recorded the distance at which initiation occurred (with respect to the body length of the actor), the closest distance between the birds, the place where the interaction occurred, the outcome of the event, the duration of the event, and the time until the next interaction took place.

RESULTS

Western Bluebirds successfully drove out the resident woodpeckers at both nests. At the Angel Burn nest, Black-backed Woodpeckers and Western Bluebirds were seen together on or within 1 m of the nesting cavity intermittently from 14 to 16 May 2015. The Black-backed Woodpeckers were not seen at the nesting cavity after 16 May 2015. At the Hause Creek nest, Black-backed Woodpeckers were photographed excavating a cavity on 18 April 2015. However, in our first video footage of that nest on 28 April 2015, only Hairy Woodpeckers and Western Bluebirds were seen at the nesting cavity. Hairy Woodpeckers were not seen after 30 April 2015.

At the Hause Creek nest, the takeover period lasted about 24 hours. Bluebirds were already present at the Angel Burn nest when we began filming, so the length of the takeover period cannot be strictly defined. We defined the end of the usurpation as the last visit the woodpecker made to the cavity before an absence of at least 24 hours. At the

Angel Burn nest, the Black-backed Woodpeckers were heard presumably excavating a new nest about 22 hours after they were last seen at the original nest.

At the Angel Burn nest, nine out of ten bluebird–woodpecker interactions occurred within the first 24 hours, and at the Hause Creek nest, six out seven of these interactions also occurred within the first 24 hours. The majority of interactions were chases (six of ten at the Angel Burn nest, four of seven at the Hause Creek nest), with the Western Bluebird being the initiator in all cases (Tables 1-1 and 1-2). Vocalizations by both bluebirds and woodpeckers accompanied 40% of all chases. In five of the ten chases, both the male and female bluebird flew directly at the woodpecker from either side with physical contact occurring (see Supplemental Videos). We observed no sexual discrimination, as both male and female bluebirds attacked both male and female woodpeckers. Woodpeckers responded with vocalizations and a defensive display with open wings but no direct chases toward the bluebirds. Woodpecker presence at the nest dropped off after the first 6–10 hours. At both nests the woodpeckers returned after 24 hours but were chased by the bluebirds and not seen afterward. All interactions described here took place immediately at or within 1 m of the nesting cavity.

Table 1-1 Numbers of Behaviors Video-Recorded during Takeover of a Nest of the Black-backed Woodpecker (Angel Burn) by Western Bluebirds

	Behavior[a]			Western Bluebird sex		
Date and time	Chase	Vocal	Both[b]	M	F	Unknown
14 May						
11:00 a.m. – 1:00 p.m.	2	1	3	0	0	0
1:00 p.m. – 3:00 p.m.	1	0	1	0	0	0
3:00 p.m. – 5:00 p.m.	0	0	0	0	0	0
5:00 p.m. – 7:00 p.m.	0	0	0	0	0	0
7:00 p.m. – 9:00 p.m.	0	0	0	0	0	0
15 May						
5:30 a.m. – 7:30 a.m.	2	1	2	1	0	0
7:30 a.m. – 9:30 a.m.	0	0	0	0	0	0
9:30 a.m. – 11:30 a.m.	0	0	0	0	0	0
11:30 a.m. – 1:30 p.m.	0	0	0	0	0	0
1:30 p.m. – 3:30 p.m.	0	0	0	0	0	0
3:30 p.m. – 5:30 p.m.	1	1	0	0	1	1
16 May						
1:30 p.m. – 3:30 p.m.	0	0	0	0	0	0
3:30 p.m. – 5:30 p.m.	0	0	0	0	0	0
5:30 p.m. – 7:30 p.m.	0	0	0	0	0	0
7:30 p.m. – 9:30 p.m.	0	0	0	0	0	0
17 May						
5:30 a.m. – 7:30 a.m.	0	0	0	0	0	0
7:30 a.m. – 9:30 a.m.	0	0	0	0	0	0
9:30 a.m. – 11:30 a.m.	0	0	0	0	0	0
11:30 a.m. – 1:30 p.m.	0	0	0	0	0	0
1:30 p.m. – 3:30 p.m.	0	0	0	0	0	0
3:30 p.m. – 5:30 p.m.	0	1	0	1	0	0
5:30 p.m. – 7:30 p.m.	0	0	0	0	0	0
19 May						
11:30 a.m. – 1:30 p.m.	0	0	0	0	0	0
1:30 p.m. – 3:30 p.m.	0	0	0	0	0	0
20 May	0	0	0	0	0	0
7:30 a.m. – 9:30 a.m.						
28 May	0	0	0	0	0	0
1:30 p.m. – 3:30 p.m.						
Total	6	4	6	2	1	1

[a]Includes only actions of the Western Bluebirds directed at woodpeckers, not those of driving off other species from the nest. Vocalizations often accompanied chases and were not always truly separate events.

[b]Both members of the pair acting simultaneously.

Table 1-2 Numbers of Behaviors Video-Recorded during Takeover of a Nest of the Hairy Woodpecker (Hause Creek) by Western Bluebirds

	Behavior[a]			Western Bluebird Sex		
Date and time	Chase	Vocal	Both[b]	M	F	Unknown
28 Apr						
6:15 p.m. – 8:15 p.m.	0	0	0	0	0	0
8:15 p.m. – 10:15 p.m.	0	0	0	0	0	0
29 Apr						
5:30 a.m. – 7:30 a.m.	1	0	0	1	0	0
7:30 a.m. – 9:30 a.m.	0	0	0	0	0	0
9:30 a.m. – 11:30 a.m.	0	0	0	0	0	0
11:30 a.m. – 1:30 p.m.	0	0	0	0	0	0
1:30 p.m. – 3:30 p.m.	0	0	0	0	0	0
3:30 p.m. – 5:30 p.m.	0	0	0	0	0	0
5:30 p.m. – 7:30 p.m.	0	0	0	0	0	0
7:30 p.m. – 9:30 p.m.	1	1	1	1	0	0
30 Apr						
5:30 a.m. – 7:30 a.m.	1	2	1	1	1	0
7:30 a.m. – 9:30 a.m.	0	0	0	0	0	0
9:30 a.m. – 11: 30 a.m.	0	0	0	0	0	0
11:30 a.m. – 1:30 p.m.	0	0	0	0	0	0
1:30 p.m. – 3:30 p.m.	0	0	0	0	0	0
3:30 p.m. – 5:30 p.m.	0	0	0	0	0	0
5:30 p.m. – 7:30 p.m.	0	0	0	0	0	0
7:30 p.m. – 9:30 p.m.	1	0	0	1	0	0
4 May						
12:30 p.m. – 2:30 p.m.	0	0	0	0	0	0
2:30 p.m. – 4:30 p.m.	0	0	0	0	0	0
4:30 p.m. – 6:30 p.m.	0	0	0	0	0	0
5 May						
4:00 p.m. – 6:00 p.m.	0	0	0	0	0	0
6:00 p.m. – 8:00 p.m.	0	0	0	0	0	0
7 May 2:30 p.m. – 4:30 p.m.	0	0	0	0	0	0
8 May 7:30 a.m. – 9:30 a.m.	0	0	0	0	0	0
Total	4	3	2	4	1	0

[a]Includes only actions of the Western Bluebirds directed at woodpeckers, not those of driving off other species from the nest. Vocalizations often accompanied chases and were not always truly separate events.

[b]Both members of the pair acting simultaneously

DISCUSSION

We have described how Western Bluebirds engage Black-backed and Hairy Woodpeckers in interference competition, keeping the woodpeckers from using their own nest by usurping the nest. The smaller Western Bluebird (23.5–31.5 g; Guinan et al. 2008) uses cooperative, tag-team chases to usurp nest from larger woodpeckers (Black-backed, 67.8–82.7 g, Tremblay et al. 2016; Hairy [northwestern U.S.], about 66–84 g, Jackson et al. 2002). In nest defense against its own species, aggression of the Eastern Bluebird (*Sialia sialis*) is sex-specific, with females directing aggression toward females, males toward males (Gowaty and Wagner 1988). In contrast, Western Bluebirds are not known to discriminate by sex when establishing and defending a nesting territory (Herlugson 1980). When another male Western Bluebird showed up at the Angel Burn nest, only the male bluebird of the pair attacked the intruding male, suggesting the female may have been fertile (Dickinson and Leonard 1996). Olsen et al. (2008) reported both members of Western Bluebird pairs defending nests against life-like models of the European Starling (*Sturnus vulgaris*) by physically attacking the model. Our results suggest that Western Bluebirds usurp nests from woodpeckers in a similar manner.

Bluebirds disperse cyclically, and individuals dispersing to exploit and colonize new habitat (such as a recently burned forest) have been exposed to higher levels of androgens during development (Duckworth 2008, Duckworth et al. 2015). Nest usurpation may be a function of maternally induced aggression and the limited number of nest cavities available in recently burned forests (White et al. 2005, Duckworth et al. 2015, Edworthy 2016).

In both cases, bluebirds took over the cavity early in the breeding season soon after the woodpeckers had finished excavating and before they had laid eggs (Hause Creek nest, 28 April 2015; Angel Burn nest, 16 May 2015). Early in the breeding season, it may be more efficient for woodpeckers to abandon a nest and excavate a new cavity rather than fight off highly aggressive bluebirds. Later in the breeding season, we observed a male Western Bluebird investigating an active Northern Flicker nest, but there were no physical altercations. At a certain point, nestling woodpeckers may be too large for bluebirds to usurp the nest, and parent woodpeckers may defend the nest more intensely as the time available for reproduction decreases later in the season (Biermann and Robertson 1981).

Usurpation of woodpecker nests by bluebirds may be relevant to management, as the Black-backed Woodpecker is a species of conservation concern in several states, including Washington (Murphy and Lehnhausen 1998, Bonnot et al. 2008). Of the six Black-backed Woodpecker nests we filmed during our pilot study, two were usurped. While we were unable to confirm whether the Hairy Woodpeckers actually usurped the Hause Creek cavity from the Black-backed Woodpeckers that excavated it, this ratio still suggests that there is competition for nest cavities and snags suitable for nesting. However, nesting Western Bluebirds may benefit woodpeckers if enough cavities are available. In our study, the male bluebird was seen chasing off other male bluebirds, and both the male and female bluebird were seen chasing Brown Creepers (*Certhia americana*) from the nesting tree. Additionally, we saw a male Western Bluebird flying at a Douglas Squirrel (*Tamiasciurus douglasii*) at an abandoned White-headed Woodpecker cavity. If nest cavities are abundant, bluebirds may inadvertently defend active woodpecker nests from other aggressive secondary cavity nesters and nest predators.

Because of its capacity for aggressiveness, the Western Bluebird is able to usurp cavities from Black-backed and Hairy Woodpeckers quickly when nest sites are limited. Therefore, the key to helping threatened woodpeckers such as the Black-backed is to manage fire regimes within forests so that there is an ample supply of snags available to supply nesting cavities for the woodpeckers, bluebirds, and the other species that depend on them for survival.

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CHAPTER II

LESSONS LEARNED FROM INVOLVING UNDERGRADUATE GENERAL BIOLOGY STUDENTS IN AUTHENTIC GRADUATE RESEARCH

Participating in undergraduate research has many benefits for students. However, it can be a challenge to extend research opportunities to every undergraduate. Here, we describe an original research opportunity offered to 937 students in a General Biology laboratory course and the impact the experience had on the participants as well as the researchers. As part of a master's thesis project addressing the ecology of woodpecker nesting, students watched videos of nesting woodpeckers and recorded the species and behavior observed. Students received extra credit for participation. In addition, a proportion of the participants voluntarily answered a questionnaire about their experience. A trained team of undergraduate researchers then validated the students' data. About 15% of students in the course participated. We found that students accurately recorded data approximately 90% of the time. Most students came away from the experience with a more positive attitude towards undergraduate research and were able to restate the main research question in their own words. However, many students had difficulty understanding their role as a data collector in the research project. Students who participated were more likely to have a higher grade than those who did not. Based on our experience, we recommend that local graduate students engage with undergraduate students in course-based research experiences. We suggest making the experience mandatory to include all students and place a greater emphasis on the process of science than on the research topic.

Keywords: graduate student collaboration, undergraduate research, course curriculum, data collection, citizen science, general biology lab

Introduction

Numerous studies have demonstrated the beneficial impacts of undergraduate research experience in preparing students for future careers in STEM fields (Zydney, Bennett, Shahid, & Bauer, 2002; Bauer and Bennett, 2003; Russell, Hancock, & McCullough, 2007). Undergraduates who participate in research usually rate their experience as highly positive, giving them a more positive outlook on STEM careers (Lopatto, 2004). Research experience often includes extensive interactions with university faculty, establishing a relationship for future references, networking opportunities, and ongoing mentorship and advice during their professional or academic career (Hathaway, Nagda, & Gregerman, 2002). In fact, students who participate in undergraduate research are more likely to complete an undergraduate STEM degree (Chaplin, Manske, Cruise, 1998; Gregerman, Lerner, von Hippel, Jonides, & Nagda, 1998) and enroll in graduate or professional school (Hathaway et al., 2002). In addition, providing more students with research opportunity early in their undergraduate education may lead to increased diversity in STEM fields. When compared to control groups that did not participate in undergraduate research, African-American students had higher undergraduate retention (Gregerman et al., 1998), and both African-American and Hispanic students had significantly higher rates of graduate school enrollment (Hathaway et al., 2002; Russell et al., 2007).

Instructors and researchers have long pushed for involving more undergraduates in authentic research experiences as part of their educational experience (Seago, 1992; Chaplin et al., 1998), however, major logistical constraints arise when trying to implement such programs. At research-focused institutions with thousands of students in

STEM majors, designing an undergraduate research program to reach all students is challenging. It takes time and effort to establish the infrastructure necessary for such programs, and most research labs do not have enough room for every interested student (Russell et al., 2007). In certain undergraduate research programs, like the National Science Foundation's Research Experience for Undergraduates program, students must meet certain criteria to be considered for admission, and even then, a random lottery sometimes determines who is accepted and who is not (Hathaway et al., 2002). Furthermore, students may need to be self-motivated to find and pursue research opportunities (Hathaway et al., 2002; Bangera & Brownell, 2014). Students may not be aware of these programs or know to seek them out; thereby, many qualified students, especially those from underrepresented groups in STEM fields, may miss these opportunities (Eagan Jr., Hurtado, Chang, Garcia, Herrera, & Garibay, 2013; Spronken-Smith, Mirosa, & Darrou, 2014). Lastly, these research experiences tend to focus on upperclassmen who, presumably, are better prepared to undertake original research after completing prerequisite courses and narrowing their field of interest (Chaplin et al., 1998). As such, some researchers suggest that these opportunities need to be introduced at the freshman and sophomore level (Russell et al., 2007; Spronken-Smith et al., 2014).

Exposing a broad range of students to undergraduate research in a 'low-risk' environment may help reduce the barrier to entry into other undergraduate research opportunities outside the classroom. Programs such as the CURE program (course-based undergraduate research experiences) have sought to address this by including diverse authentic research experiences in courses taken for credit (Bangera & Brownell, 2014). To effectively reach the most students, the authors argue that CURE-type programs should be implemented in courses at the introductory level. Here, we present our own findings of introducing undergraduates to authentic research at the introductory level through collaboration with a local graduate student. We conducted an authentic scientific research project in a General Biology laboratory course at Utah State University with nearly 1,000 students. Specifically, we examined the validity of using data collected by a large number of previously untrained undergraduates, the impact on students who participated in the project, and the logistics of incorporating such a project into the curriculum.

Methods

Project

The project we implemented into the General Biology lab course was part of a master's thesis of a graduate student in the Department of Biology at Utah State University. The project was focused on the nesting ecology of woodpeckers in the Eastern Washington Cascades. The research sought to answer how interactions between nest competitors, nest predators, and parent woodpeckers influenced woodpecker and nest competitor nesting behavior and success. We used video cameras at 30 woodpecker nests to capture feeding and competitor/predator behavior. We had approximately 15,000 hours of daylight footage.

Nine hundred thirty-seven students were introduced to this project three weeks into the General Biology laboratory course. In half of the 32 lab sections, the project was introduced by the graduate student in charge of the project, and in the other half, by the teaching assistant (TA) for that section. The presentation focused on the research question, the study species, and how the data would be used by the U.S. Forest Service to manage forests and animal populations. Students watched several instances of predation and nest usurpation that had been recorded during the study. In addition, the presenter discussed opportunities to engage in undergraduate research at USU and how participating in research might benefit students. The initial introduction of the project was approximately 10 minutes long for each lab section. After this introduction, students were reminded every week of their opportunity to participate.

We encouraged participation in this project by offering extra credit, which would increase a student's overall grade by 2% in the course. Students received the extra credit if they read through a detailed protocol, watched one two-hour video while recoding data, and returned their datasheet to the TA the next week.

Logistics

Students downloaded videos off USB flash drives onto their personal computer. Each section had two USB's with two videos each, for a total of four videos available for download per lab section per week. Each video file was approximately 4 GB and took students five minutes to download. Upon download, students initialed a checkout sheet that had the name of their nest and video file number; this helped us keep track of the number of times each video was watched. Enough videos were provided throughout the course of the semester for each student to have the opportunity to watch one.

Students picked up a datasheet along with a detailed protocol to follow and a photographic guide to the most common birds and animals seen in the area. The protocol instructed students on how to record the time of entrance and exit for each animal seen, the species of each animal seen, each animal's behavior, sex, as well as any other additional notes. There were five behavior codes: on the nest, in the nest, feeding nestlings, in the background, or chasing another animal, that helped track interactions competitors, predators, and woodpeckers around the nest and one another.

We collected returned datasheets at the end of the week, and a research team of trained undergraduates reviewed the videos to correct any mistakes made by the General Biology students. At the end of each week, we deleted video files that had been checked and downloaded new files so that there were always four new videos for each lab section every week. One 4 GB video file took approximately 20 minutes to download onto one USB.

Surveys

When students checked out their videos, they were encouraged to pick up a survey that asked them about this research experience. The surveys were introduced in each lab section by an individual not involved in grading the course to ensure students would not be coerced to participate (USU IRB protocol #7767). Students were asked to give their major but no other identifying information. The survey was completed voluntarily, and students did not receive additional credit for completing the survey. The survey asked if they had been aware of undergraduate research opportunities beforehand, how their participation affected their view of undergraduate research opportunities, who introduced the project to their lab, and any other comments. Students were also asked to restate the main research question in their own words and how their participation contributed to the project (Table 2-1). If students completed the survey, they returned it to their TA in a sealed envelope.

Table 2-1. Survey questions along with given answer options (if applicable). Note that Questions 1 and 2 were regarding the student's ability or willingness to participate in the survey and were not a part of any analysis.

Survey Questions	
Question	*Answer Options (blank if no given options)*
3. What is your current major?	
4. Before participating in this project, did you know about opportunities for undergraduate research?	Yes No
5. Did your participation in this project influence your interest in undergraduate research?	A: This project increased my interest in participating in undergraduate research B: This project decreased my interest in participating in undergraduate research C: I already wanted to participate in undergraduate research, and this project did not influence me. D: I did not want to participate in undergraduate research, and this project did not influence me.
6. In your own words, what was the main research question this project was addressing?	
7. How did your participating in this project contribute to answering the research question?	
8. Did the graduate student research, Sammy Cowell, or another teaching assistant	Sammy Cowell Other person

explain the project to your lab section?	I don't remember
9. Comments on the experience:	

Scoring of Surveys

After the end of the semester, student surveys were collected and scored together by two of the authors. We grouped student majors (Question 3) as either 'biology', 'non-biology science', or 'non-basic science' majors based on their college affiliation within Utah State University (Table 2-2). Questions 6, 7, and 9 were subjective and open-ended (Table 2-1). Questions 6, regarding the student's understanding of the research question, was scored on a 0-3 scale (see Table 2-3 for specifics on scoring). Question 7, regarding the student's understanding of their contribution to the project, was scored in two parts: 1) whether the students understand that they were collecting data for this project, and 2) whether the students understand how their data would be used in the project (Table 2-3). General comments (Question 9) were scored as negative, neutral, or positive. Questions 4 and 5 were multiple choice answers and did not need to be scored.

Table 2-2. Grouping of majors. The placement of majors within the groups is not based on the content of the major, but rather their affiliated college within Utah State University.

Major	**Group**
Veterinary Science Human Biology Conservation Biology Wildlife Science Plant Science Nutrition Science Forestry Biotechnology Public Health	BIOLOGY
Bioengineering Biochemistry Chemistry Physics Mathematics	NON-BIOLOGY SCIENCE
Nursing Business Psychology Human Movement Science Undeclared Economics	NON-BASIC SCIENCE

Table 2-3. Scoring of Questions 6 and 7. Question 7 was scored in two parts: 1) Did the students understand that they were collecting data for this project, and 2) did the students understand how their data would be used in the project? All examples are direct quotes from student surveys.

Scoring of Survey Questions			
Question	*Score*		*Reasoning*
6. In your own words, what was the main research question this project was addressing?	0		No response or an extremely generalized answer (e.g. ‘What happens to woodpeckers’).
	1		Student mentioned something about how this project was studying woodpecker behavior (e.g. ‘How do woodpeckers behave in the wild’).
	2		Student stated that this project was studying the nesting success of woodpeckers (e.g. ‘What are the nesting factors of woodpecker that contribute to their success’).
	3		Student understood that this project was studying the behavior of nesting woodpeckers and their competitors and predators and how that behavior affected nesting success (e.g. ‘What animals in the woodpecker’s community have an [e]ffect on their successful nesting and raising young’).
7. How did your participating in this project contribute to answering the research question?	Data	No	Student did not display any understanding of how they were collecting data.
		Conceptual	Student did not explicitly mention the term ‘data’ in their response but used other terms such as ‘observed’, ‘recorded’, ‘collected’, ‘analysed’, ‘documented’, etc. that indicated they had some understanding in their role in collecting data.

		Yes	Student explicitly mentioned the term ‘data’ in their response.
	Specificity	0	No response or no understanding of how their data would be used in the project (e.g. ‘I knew what happened in those 2 hrs of footage’).
		1	Student understood that their data would, on some level, be used to help study woodpeckers (e.g. ‘Recorded what went in and out the birds nest’).
		2	Student understood their data would be used to help explain nesting success of woodpeckers (e.g. ‘It helped show ways that contribute to the success/fails of woodpecker nesting’).
		3	Student understood that their data collection would be a part of the larger database reviewed by the researchers on woodpecker and competitor/predator behavior and nesting success (e.g. ‘I recorded every animal that was close to the nest so eventually someone else can crunch the numbers and see if the frequency of this species has an [e]ffect on the woodpeckers’).

Analysis

We analysed the accuracy of student data collection by measuring for criteria from 50 randomly selected datasheets against the corresponding datasheets of our trained research team. We scored these criteria as a binary, yes or no, variable. First, were the students within +/- five seconds of the entrance and exit times of the animal into the frame of the video (scored as separate categories)? Second, did the students write down the correct species code? Third, did the students record the correct behavior code?

For the species, we calculated how likely it was for a student to misidentify a species given they had already misidentified one. For events with misidentified species, we graded them on severity, with Tier I being a less severe mistake (e.g. coding a rodent species as a different rodent species) and Tier II being a more severe mistake (e.g. misidentifying the focal woodpecker species of the nest). We created a contingency table to test for an interaction between these Tiers and the location of the event.

We also calculated the average number of false positives and false negatives per video. An example of a false positive is a student watching an insect fly through the frame and recording it as a bird. An example of a false negative is a student missing an animal either flying or running through the frame, at the nest or in the background. We calculated the frequency of the behavior codes within these false negatives to determine the egregiousness of the error (i.e. did a student miss a bird flying far away in the background compared to missing an animal at the nest). We calculated the conditional probability of an additional false negative given one false negative.

Finally, we created contingency tables to examine how the frequency of coding errors and false negatives/positives was impacted by the event type in the video (e.g. background event versus event at the nest). We graded these errors by severity and placed them in one of two categories: Tier 1 errors were incorrect codes that were still at the same location in the video (e.g. ‘in the nest’ instead of ‘on the nest”), whereas Tier 2 errors were codes that described events at a different place in the video (e.g. ‘in the nest’ instead of ‘background”) or instances when students did not use a code that we had given them (e.g. ‘lands on the tree’ instead of ‘onne’ for on nest tree).

To measure the impact of this experience on the students, we analysed results from the survey as well as the grades of those who participated in the project compared to those who did not. We ran a logistic regression model to see how a student’s major impacted their previous knowledge of undergraduate student research opportunities. We also ran stepwise multinomial regression models to see how a student’s major, previous knowledge of undergraduate research opportunities, and who presented to them affected levels of interest afterwards (Question 5), their ability to restate the research question (Question 6), their ability to understand their role in data collection (Question 7), and their comment ratings, using Akaine’s Information Criterion (AIC) to choose the best fitted model. For each model we also calculated McFadden’s pseudo-R^2. Student responses with blank information or an “I don’t remember” in Question 8 (who presented) were left out of model analysis.

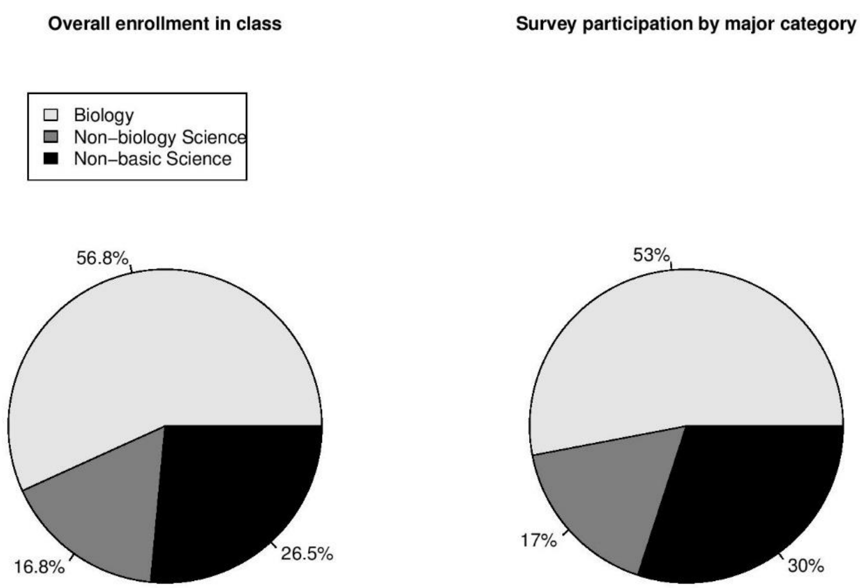
At the end of the semester, we removed the names of students from the gradebook and calculated the average grade of students who did not participate and the average grade of students who did participate before the extra credit points were added to their grade. We ran a mixed-model with lab section and TA as random effects to compare the grades of the two groups of students. All statistical software computing was conducted in R 3.4.0.

Results

Accuracy

Out of 937 students, 149 students participated in the research, and 100 students returned useable surveys (four students returned surveys but did not answer questions). Participation rates from the survey did not vary significantly among the three groups of majors (biology, non-biology science and non-basic science) in the class (Pearson's Chi-squared test, χ^2= 0.65231, df = 2, p-value = 0.7217, Figure 2-1).

Figure 2-1: Enrollment in the General Biology Course by major (n = 937) and survey participation by major (n = 100).



Students accurately recorded data 89.23% of the time on average across the four categories that we tested for student accuracy. Students recorded an accurate (within +/- five seconds) entrance time 92.40% of the time, an accurate exit time 91.05% of the time, the correct species 90.03% of the time, and correct behavior 83.45% of the time.

When students misidentified a species, 50% of the time, they were likely to misidentify a species at least one another time. Out of the 59 events with misidentified species, 48 of these events came from students with at least two misidentified species, with one student misidentifying 13 out of 14 species. If this extreme outlier was excluded, student accuracy on species identification rose to 92.04%. Misidentified species came from approximately equal number of background and nest events. Most incorrect species were classified as Tier II misidentifications, but there was not a significant interaction of Tier ranking and event location (Table 2-4, Fisher's Exact Test, $p = 0.26$).

Table 2-4: Incorrect Species based on severity (Tier) and Location, excluding one outlier student.

	Background	At Nest
Tier I	6	3
Tier II	14	21

Events at the nest were nearly 33 times more likely to be incorrectly coded for behavior when compared to events away from the nest (Fisher's Exact Test, Odds Ratio (OR) estimate = 32.8, $p < 0.001$, Table 2-5a). Most of these incorrect errors were insignificant Tier 1 errors. However, after removing Tier 1 errors, we still found that students were over four times as likely to commit Tier 2 errors with events at the nest (Fisher's Exact Test, OR estimate = 4.35, $p = 0.0469$, Table 2-5b.). We found that students were twice as likely to miss background events than nest events (Fisher's Exact Test, OR estimate = 2.17, $p = 0.0104$, Table 2-5c). Across the 50 videos viewed for validation, there was an average of 1.08 false negatives per video and 1.98 false positives per video. If the student had one false negative, there was a 57.14% probability that there would be another false negative.

Table 2-5a: Number of correctly scored and incorrectly scored events by event type.

	Incorrect	Correct
Away from nest	2	207
At nest	83	261

Table 2-5b. Number of Tier 2 errors by event type.

	Incorrect	Correct
Away from nest	2	207
At nest	11	261

Table 2-5c. Number of missed events (false negatives) by event type.

	Missed Events	Events Scored
Away from nest	29	209
At nest	22	344

Surveys

Most students reported that they were aware of undergraduate research opportunities (65%). There were nearly significant differences in knowledge of undergraduate research opportunities for students in biology and non-biology science majors ($p = 0.0772$, 0.0598, respectively), but not for non-basic science majors ($p = 0.6169$; $R^2 = 0.04$). We found that non-biology science majors were more knowledgeable of research opportunities than biology majors (Figure 2-2). Some students reported that they were already interested in engaging in undergraduate research (34%), and many said this project increased their interest in undergraduate research opportunities (56%). A small number of students reported that they had no interest in undergraduate research (7%) or that this project decreased their interest (3%, Figure 2-3).

Figure 2-2: Student response to Question 4 of if they had previous knowledge of undergraduate research opportunities grouped by major.

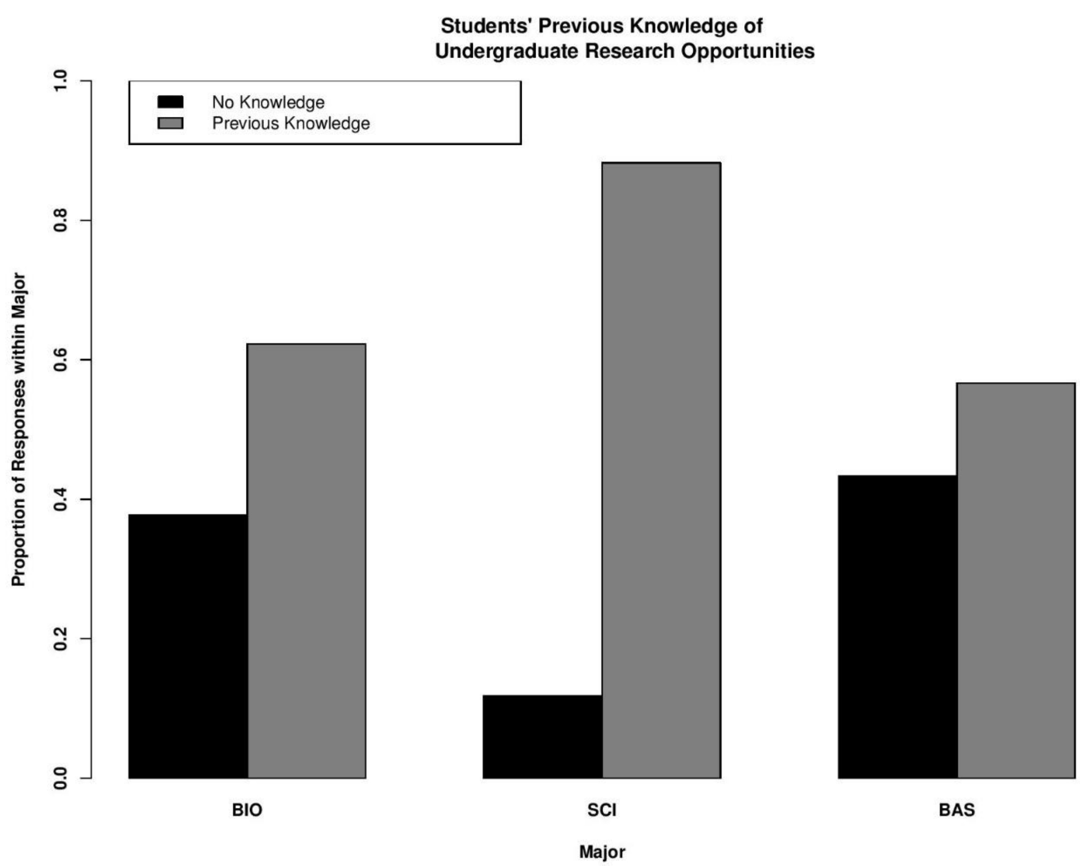
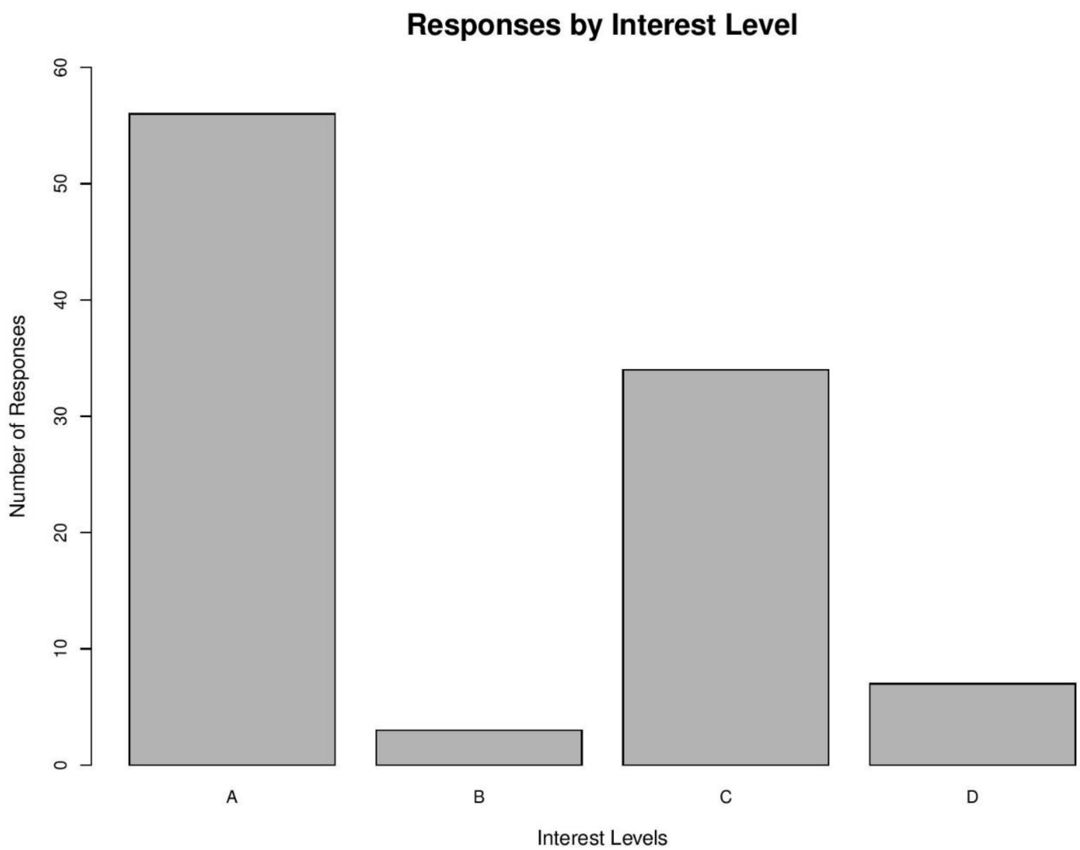


Figure 2-3: Student response to Question 5 of how their participation in the project influenced their interest in undergraduate research. A: This project increased my interest in participating in undergraduate research. B: This project decreased my interest in participating in undergraduate research. C: I already wanted to participate in undergraduate research, and this project did not influence me. D: I did not want to participate in undergraduate research, and this project did not influence me



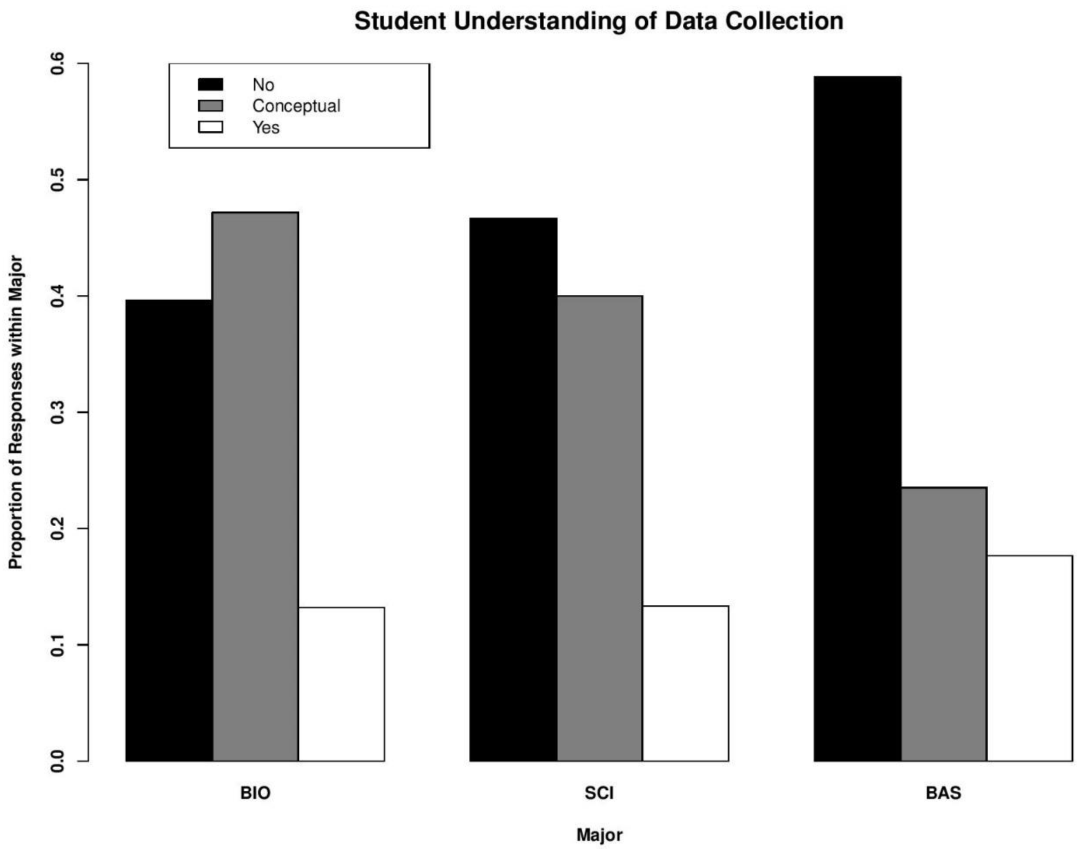
As some interest level categories had low responses, we approached our analysis in two different ways. When combining positive (A and C) and negative (B and D) answers (Table 2-1), only students' major was included in the final model. Students largely reported positive feelings (90%). When compared to biology majors, non-biology science majors were more likely to report positive feelings (OR > 100, $p < 0.001$, $R^2 = 0.21$), while non-basic science majors were less likely (OR = 0.11, $p < 0.01$). However, all majors largely reported positive feelings (Table 2-6). When combining 'changed interest levels' (A and B) and 'unchanged interest levels' (C and D), more students were more likely to have changed their interest (59%). The final model included student's previous knowledge of research opportunities and who presented to them; these factors were nearly significant ($p = 0.0549$, $p = 0.0774$, respectively, $R^2 = 0.07$).

Table 2-6. Undergraduate student response by major and interest (positive or negative) interest levels after participation.

	Positive (A and C)	Negative (B and D)
Biology	42	2
Non-biology science	15	0
Non-basic science	17	7

Most students received a score of either a 2 or 3 (63%) when asked to restate the research question. When asked about their role in the project, 14% of students explicitly mentioned the term ‘data’, 41% of students displayed a conceptual understanding of their contribution to data collection, and 45% did not demonstrate any understanding of data collection. Compared to biology and non-biology science majors, non-basic science majors had the largest proportion of students unable to demonstrate an understanding of data collection (Figure 2-4). Most students (59%) received a low score of 0 or 1 (the highest possible score being a 3) for understanding how their role factored into the overall project. In the comments section, 42% of students did not leave a comment, 5% students left a neutral comment, 14% students left a negative comment, and 39% students left a positive comment.

Figure 2-4: Student scores of how they understood their role as data collectors as determined by their responses to Question 7: How did your participating in this project contribute to answering the research question? Students with 'Yes' score explicitly mentioned the term 'data'. Students with a 'Conceptual' score did not explicitly mention the term 'data', but mentioned other terms such as 'collected', 'analyzed','documented', etc. Students with a 'No' score did not give any indication that they understood their role as data collectors



When testing models on the students' interest level after the project, their ability to restate the project's objectives, or their understanding of how their data would be used for the project, only one model (ability to restate the research question) differed from the null model by including an explanatory variable (previous knowledge, however this was highly non-significant, all p's > 0.85). A model of student ratings included presenter in the final model; this was barely non-significant (p's > 0.05, $R^2 = 0.05$). The ratios of positive to negative comments were similar for the graduate student researcher (24:9) and the TA (9:3). However, when combining neutral/none comments and positive/negative comments, students who learned about the project from the graduate student researcher were over four times as likely to provide a positive or negative comment (OR = 4.22, $p < 0.01$, $R^2 = 0.09$).

Students earned two points of extra credit (2% of total possible points) for completing a video analysis. Mixed-models showed that the teaching assistant (TA) variable was not a significant predictor of student's grades (standard deviation of 0), and there was no significant difference between the null model and the model including lab sections (ANOVA, $\chi^2 = 0.3374$, df = 1, p = 0.5613). The grades of students who participated were 2.33 points higher before adding the extra credit points than the grades of students who did not participate (Wilcoxon rank sum test with continuity correction, W = 53381, $p < 0.001$).

We spent 2.5 hours presenting the project to 16 lab sections, two hours preparing the protocol materials, and two hours per week for six weeks managing video files and student data sheets for a total of 16.5 hours of effort. Trained undergraduate researchers watched the identified sections of the video files to verify or correct the general biology students' work. These undergraduate researchers could process more video files per week as they did not have to spend two hours watching each video file to identify the relevant sections. We calculated that involving the general biology students in our research saved 283.5 hours of effort for the research team.

Discussion

In this study, undergraduate students with minimal training provided accurate analysis for a large-scale, video-based project. In two of the three criteria we examined, students were 90% accurate. Student accuracy of species identification is comparable to other citizen science projects that have attempted similar goals (see Delaney, Sperling, Adams, & Leung, 2008). Furthermore, many of these inaccuracies came from localized sources (e.g. the student who misidentified 13 out of 14 species), making it easier to weed out "inaccurate" recorders from the majority of students who were "accurate" recorders.

The least accurate category was the behavior codes. However, even in this instance, out of the 85 miscoded behaviors, 72 were Tier 1 errors involving the nest ('feeding nestlings' vs. 'inside nesting cavity"), with 27 of these errors coming from one student. In our project, it can be difficult to determine which code to use, even for trained researchers, as it is not always obvious whether a parent is carrying a small food item to the nest and then feeding the nestlings inside. Events around the nest had more Tier 2 errors, with six of these errors due to students writing a correct action but not correct code (e.g. 'flew into the nest' instead of 'inne' for in the nest). Five of these six errors came from one student.

False negatives provide a more difficult challenge in that they are not easily caught by trained observers since they are reviewing video segments identified by the students. Most of the false negatives (54.72%) in our analysis were background events, not directly concerned with the nesting cavity or tree. This reduces the amount of meaningful false negatives from 1.08 to 0.49 false negatives per video. Furthermore, as datasheets with false negatives were more likely to produce another false negative, we conclude that most of false negatives came from 'localized' sources, much like species misidentifications (e.g. 13 out of the 51 false negatives came from one student). This can be encouraging as trained undergraduate researchers reported that when they noticed one false negative, they began to comb through the entire video to ensure there were no other false negatives, thereby reducing the amount of missed false negatives. False positives do not significantly impact data quality as they take little time to examine and discount.

Using undergraduate students with minimal training can be a legitimate method for sound data collection, comparable to the widespread collaboration with citizen scientists in research. Large groups of volunteers, numbering hundreds or even thousands, collect or analyse large datasets with minimal training (Bonney et al., 2014; Danielsen et al., 2014). Our results are especially encouraging in that students received no direct guidance from the researchers after the initial presentation and still obtained highly accurate results by simply reading the protocol. Presumably, projects with more time spent training and hands-on guidance will produce more accurate results from previously untrained students or volunteers.

Students who participated in this project had a largely positive experience. Of the students who changed their opinion towards undergraduate research, more students indicated that the project increased their desire to participate in undergraduate research than decreased their desire. These results are nearly identical with studies focusing on student attitude towards postgraduate education after participating in undergraduate research (Lopatto, 2004), but with much less time and investment when compared to a summer internship within one research lab. Non-basic science majors were not as positive towards future research opportunities compared to biology majors, but this is because biology major responses were overwhelmingly positive (51/53) when compared to the still largely-positive responses of non-basic science majors (22/30). We could not test if positive student responses were simply due to receiving extra credit, but future studies could do so by offering no credit in one semester and extra credit in another.

Many participants could restate the research question in their own words. We are encouraged by this result as the only exposure to the research question was a 10-minute presentation and the printed materials distributed with the video files. However, when asked about their role in collecting data for the project, only about half of the students demonstrated knowledge of the importance of data collection in original scientific research, and fewer than half of the participants recognized their role in the research project. Non-biology science majors struggled in particular, with 10 out of 17 of their answers failing to mention anything about data. Several students stated that they did not contribute to the project because there was minimal or no activity in their video. These students did not understand that 'no data' recorded is still useful information. Based on our surveys, we find that the concept of data collection is a step of the scientific method that is poorly understood by undergraduate students, even in STEM majors. Other studies working with citizen scientists have found that while volunteers gain understanding of their particular subject matter, they still display a deficiency in understanding a basic concept of the scientific process (Brossard, Lewenstein, & Bonney, 2005). Therefore, we suggest, along with Brossard et al. (2005), that the scientific process be emphasized when introducing authentic research projects to undergraduates, especially within laboratory courses designed to introduce students to research.

We found TAs and a graduate student researcher were equally effective in explaining the scope and significance of the project to students. The only effect of presenter we found was that students who learned about the project from a graduate researcher were more likely to provide open-ended comments in survey. Students may see a research project as simply a part of the course when presented by their TA, and are thus more indifferent.

Students who participated in the research had a significantly higher mean grade than those who did not participate. Those interested enough to participate in research may already possess higher intrinsic motivation to perform well in academic settings (Noels, Clément, & Pelletier, 1999; Lin, McKeachie, & Kim 2003). Another study found that those who participated in a voluntary research project for extra credit already had higher grades and scored higher on several academic measures than those who did not participate (Padilla-Walker, Thompson, Zamboanga, & Schmersal, 2005). Thus, voluntary exposure to research may not target underperforming students who could potentially benefit the most from such exposure.

The weight of extra credit could be increased in order to increase participation. Many students complained that watching a 2-hour-long video was not worth their time for ‘only two extra credit points’. However, offering extra credit may not be an efficient method to help lower-achieving students reach educational goals (Padilla-Walker et al., 2005). Just over 15% of students in the course participated in our research. Thus, instead of offering more extra credit for a research opportunity like this in the future, incorporating authentic research projects as a mandatory part of the curriculum may be more effective to help all undergraduates experience authentic research and reach desired educational learning outcomes.

It has been long known that processing, synthesizing, and restating of scientific facts and principles is an important cognitive step in a student’s scientific education

(Seago, 1992; Chaplin et al., 1998), and research projects such as this provide a perfect opportunity for students. Several students commented on how this educational, research-based experience prepared them for their future careers. One student wrote:

> ‘I really enjoyed participating in this. As a wildlife sciences major, this could very easily be a big part of my life and career in the future. Overall a very interesting and enlightening project.’

Another student commented, ‘It was interesting to see how biological research is conducted’, and one more stated, ‘This was fun! It made me realize the huge amount of time that goes into research and I appreciate it a lot more now.’ Projects do not need to be directly related to a student’s major or interest to have positive impact, as expressed in this comment: ‘This experience got me excited to participate in research in my field of study - cancer.’ Additionally, these projects do not need to be limited to STEM fields; almost 30% of our participants were from non-STEM majors. As one student commented, ‘I enjoyed [this project] and I wish as an economics major there were more school sponsored research projects in the business dept.’

In conclusion, incorporating this project into an undergraduate General Biology laboratory course appeared to benefit all parties involved. The researchers save almost 300 hours of work, and students expressed positive attitudes towards undergraduate research. Original research projects should be supported across all academic fields to encourage critical and logical thinking skills for all undergraduates, which is possible in a collaboration between graduate student and in-course undergraduates.

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CHAPTER III

USING CONTINUOUS VIDEO MONITORING TO DOCUMENT SAME-SEASON NEST WEB DYNAMICS BETWEEN PRIMARY CAVITY EXCAVATORS AND SECONDARY CAVITY USERS

ABSTRACT

Woodpeckers serve as the primary cavity excavators (PCEs) in temperate forest ecosystems, with secondary cavity users (SCUs) dependent on these cavities for their own nesting success. This creates dynamic nest webs within a community as PCEs excavate nests and SCUs compete for these nests. Research on the dynamics of these nest webs is not new, however, little work has been done to determine how direct interactions around nesting cavities influence the behavioral response and interactions between PCEs and SCUs, especially within the same season. Here, through the use of continuous video monitoring, we document direct behavioral interactions at the nests of four PCE species and SCUs in the Eastern Washington Cascades and how they influence nest web dynamics. Overall, fourteen out of thirty-one PCE nests we monitored were reused within the same season by four species of SCUs, with Western Bluebirds being are most common SCU. We found that some nests were reused within minutes to hours of vacancy by PCEs. However, we found no significant predictors of nest reuse or SCU presence at nests. Parent PCEs responded less aggressively to avian SCUs than to rodent SCUs, predators, and other PCE species. Our video-based study provides a new window into behavioral interactions in the nest webs and same-season nest reuse, but it is limited by its scope. Thus, we recommend additional video studies examining behavioral interactions around the nest and how it affects nest reuse within a season.

Keywords: Nest webs, video surveillance, same-season, primary cavity excavator, secondary cavity user.

INTRODUCTION

In temperate forest ecosystems, woodpeckers are the primary cavity excavators (PCEs), creating nesting sites that are later used by many species of birds and mammals (Raphael and White 1984, Martin and Eadie 1999). Both rodent and avian secondary cavity users (SCUs), unable to excavate their own nests, compete for vacant cavities to use for their own nests and roosting sites (Martin and Eadie 1999, Aitken et al. 2002). Thus, PCEs act as ecosystem engineers in creating these new nesting sites and introduce new nest webs into a community (Martin et al. 2004, Tarbill et al. 2015).

Nest webs have been compared to food webs in that there is a central resource produced within a community (nesting cavities), a hierarchy of competitors for this resource (PCEs and SCUs), and ecological connections among competitors and predators (Martin and Eadie 1999, Aitken et al. 2002). However, these nest webs differ from food webs in that PCEs produce the nesting cavity from raw materials (i.e. trees) and may defend the nest from other PCEs and SCUs (Cockle et al. 2012). SCUs may usurp active nests from PCEs, driving parents away and potentially killing their offspring (Loeb and Hopper 1997, Vierling 1998, Frye and Rogers 2004, Kozma and Kroll 2012, Cowell et al. 2017). Rodents have been identified as both SCUs and nest predators (Paclik et al. 2009). Thus, the direction and hierarchy of these interactions is convoluted and complex.

Research on the relationships between PCEs and SCUs is not new (Martin and Eadie 1999, Aitken et al. 2002, Martin et al. 2004, Tarbill et al. 2015, Altamirano et al. 2017), however, little work has been done to determine how direct interactions around nesting cavities influence the behavioral response between PCEs and SCUs (Paclik et al. 2009). Previous studies of nest webs focused on documenting species involved in the nest-webs, correlations between PCE and SCU abundance, frequency of nest re-use, and environmental factors affecting nest selection. In western coniferous forests, most evidence of SCU competition is anecdotal or indirect, and continuous video surveillance has been encouraged in order document interactions among members of the nest web (Packlik et al. 2009). We monitored PCE nests with video cameras and compared how PCE parents respond to SCU presence, and factors associated with nest reuse. We monitored nests of four PCE species in the Eastern Washington Cascades: Black-backed Woodpecker (*Picoides arcticus*), White-headed Woodpecker (*Picoides albolarvatus*), Hairy Woodpecker (*Picoides villosus*), and Northern Flicker. These species are PCEs found in post-fire habitats throughout the region (Haggard and Gaines, 2001). The goal for this study was to construct and interpret nest web relationships among the four PCE species and the SCUs and predators that interacted with their nest. This study was part of a larger study investigating whether rodent predators reduced nesting success in woodpecker species in the study area. In the context of interactions at the nest, we put forward two main objectives: (1) Identify variables (habitat, time of year, presence and behavior of PCEs, SCUs, and predators) that predict within nest season reuse in western coniferous forests, and (2) understand the effects of SCU presence, predator presence, habitat, and seasonal variables on the nesting behavior of PCEs in western coniferous forests.

METHODS

Field Methods

Nest monitoring. Video cameras were set up near PCE nests during the 2016 breeding seasons. Nests were located in post-fire coniferous forest habitat throughout the Naches

Ranger District, Okanogan-Wenatchee National Forest in Washington State (approximately 46º 45′ N, 120º 58′ W). These post-fire habitats were the result of prescribed fires by the U.S. Forest Service from 2006 to 2015. Fires burned with mixed-severities, creating a mosaic of small (0.1-24.2 ha) severely burned (~80-90% canopy mortality), and lightly burned (~0-10% canopy mortality) patches in an otherwise live forest (Lorenz et al. 2015, Cowell et al. 2017). Forest composition varied by aspect, elevation, and distance from the Cascade Crest and most forests were dominated by a mixture of ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), and Grand Fir (*Abies grandis*).

We began monitoring on 15 April 2016 and concluded monitoring on 6 July 2016. Nests were monitored for one-week periods with approximately seven days in between monitoring periods. When nests were not monitored with videos, they were checked every 3-4 days to confirm activity or failure. We used Panasonic camcorders (model HC-V160, Newark, NJ, USA) with LiPolymer batteries (model 1055275-2C) manufactured by Mogen Industrial Limited (Shenzhen, Guangdong, China). Cameras were mounted inside of a black PVC pipe on a tree 20-50 m from the nesting cavity. We replaced the 64 GB SD card and camera battery once a day.

Rodent and avian counts We visited each nest three times in July between 06:00 and 11:00 after all PCE species had finished nesting to assess rodent and avian SCU relative abundance. We conducted counts after the nesting season to avoid affecting nest outcomes. We conducted counts for 15 minutes at each point, recording every rodent and bird heard or seen, distance from the nest, and the time it was detected. We did not conduct counts during strong winds or rain. For each nest, we conducted counts from

06:00 to 11:00. We used the maximum number of rodents and birds seen on any count in our analyses as this value indicated that at least that many were present at the site.

Nest reuse. We determined nest reuse by visiting nests after the last PCE nestling fledged. Nest reuse was determined based on either evidence of nesting material in the cavity or observations of a SCU entering the cavity after fledging (either observed in person or on camera). If we lacked direct evidence of the SCU species, we inferred species identity through indirect evidence, such as nesting materials only used by certain species (Tarbill et al. 2015).

Vegetation. We conducted vegetation surveys after the nesting season to avoid affecting nest outcomes, following Martin et al. (1997) and Dudley and Saab (2003). We measured snag DBH (tree diameter at breast height, ~ 1.4 m), snag height, and cavity height. We measured habitat variables within a 0.04 ha plot around the nesting snag and divided the plot into four quadrants using the cardinal directions as dividing lines: number of dead trees, number of cavities in the nest tree, number of total cavities in the plot, and canopy cover. In each quadrant we measured the DBH of any trees >1.4 m and estimated percentage of the ground covered by shrubs and coarse woody debris (CWD), as these are important habitat variables for rodents (Loeb 1999, Converse et al. 2006).

Behavioral scoring. We used over 200 naïve along with 13 trained undergraduate students to score the videos. We randomly selected individual days of filming to be scored from each PCE nest, and only videos from daylight hours were used. Video files were generally two hours long. Many of these videos were initially scored by naïve undergraduates as class projects. The periods of activity in the videos were then watched by a group of thirteen trained undergraduates to verify the scoring. The accuracy of naïve undergraduates was 89.23% (Cowell et al. *in review*).

We trained 13 observers in the following protocol. Observers recorded every vertebrate species that entered the frame of the camera, the entrance and exit time, sex of the animal, and one of five behavioral codes: chasing, feeding nestlings, in the nest, on the nest tree, in the background. We defined a chase as any one animal or group of animals lunging at or pursuing another animal or group of animals. We defined "in the nest" as being in or on the rim of the nesting cavity. We defined "on the nest tree" as being on any part of the nesting tree. And, we defined "in the background" as within the frame but not directly interacting with the nesting tree. Species were classified either as the parent PCEs, avian SCUs, rodent SCUs, predators (species that had been observed on video attempting to depredate nests), or other non-parent PCE species. Observers recorded if parent PCEs were present when a non-parent animal was in the frame and the recipient of a chase.

During the first three weeks of training all scoring was verified by SDC. Throughout the project, multiple students were given the same video file to watch to calibrate scoring accuracy. SDC reviewed some videos to minimize errors.

Analysis

Principle Component Analysis. We conducted Principle Component Analysis to reduce the dimensionality of the vegetation variables, clustering them into three clusters (Table 3-1). Each nest was given a numeric score for each of the clusters.

Table 3-1: Covariates used in models for nest reuse by SCUs, or presence of PCEs and SCUs in Central Washington in 2016, with the type of variable and its specific definition.

Variable	**Variable Type**	**Description**
Cluster 1	Vegetation	Reduced-dimensionality vegetation variables describing the availability of cavities or cavity potential (the number of dead trees, number of cavities in the nest tree, and number of total cavities in the plot).
Cluster 2	Vegetation	Reduced-dimensionality vegetation variable describing the other vegetation in the plot (shrub cover, canopy cover, CWD).
Cluster 3	Vegetation	Reduced-dimensionality vegetation variable describing the height (tree height, cavity height).
Parent PCE presence	Behavioral	Arcsine-transformed variable representing proportion of time parent PCEs spent at nest in all videos analyzed for that nest.
Avian SCU presence	Behavioral	Arcsine-transformed variable representing proportion of time avian SCUs spent at nest in all videos analyzed for that nest.
Rodent SCU presence	Behavioral	Arcsine-transformed variable representing proportion of time rodent SCUs spent at nest in all videos analyzed for that nest.
Date ended	Seasonal	Calendar date the nest ended (fledgling or failure).
Day of nesting cycle ended	Seasonal	The number of days from estimated date of the first egg-laying that the nest ended (fledgling or failure).
SCU counts	Point counts	The maximum number of SCUs (avian, rodent) detected at each nest during counts.
Nesting PCE species	Other	Species of nesting PCE (Hairy Woodpecker, Black-backed Woodpecker, White-headed Woodpecker, or Northern Flicker).
Guild type	Other	The guild type (Parent PCE, Avian SCU, Rodent SCU, Predator, Non-parent PCE), to which any individual animal belongs. Animals not belonging to any of the above guilds were excluded from analysis.

Presence. We defined presence at the nest as the proportion of time any animal from a particular guild (parent PCE, rodent SCU, avian SCU, predator, non-parent PCE) was seen at the nest compared to the total number of video hours analyzed for that nest. In our final analysis, we used arcsine square-root transformations of these proportions, as rodent and avian SCU presence were close to 0 at multiple nests.

Objective 1. We used logistic regression models to test if nest reuse was affected by different vegetation, behavioral, seasonal, and count explanatory variables (Table 3-1, Models 1-6 in Table 3-2). We used generalized linear regression models to see if rodent SCU presence and avian SCU presence at the nest were affected by different vegetation, behavioral, seasonal, and count explanatory variables (Table 3-1, Models 7-13 in Table 3-2).

Table 3-2: All tested models of nest reuse by SCUs, presence of PCEs and SCUs, or parental PCE response to different guilds in central Washington in 2016. Models are arranged by response variable and corresponding explanatory variables. For logistic regression models, likelihood ratio p-values are reported. Models with only one variable are included only when they are significant ($P < 0.05$) or close to significant ($P < 0.07$).

Model Number	**Response Variable**	**Explanatory Variable(s)**	**p-value**
		Objective 1	
1	Nest Reuse (yes/no)	Reduced-dimensionality vegetation variables (Clusters 1,2,3)	0.899
2	Nest Reuse (yes/no)	Parent PCE presence, Avian SCU presence, Rodent SCU presence	0.9690

3	Nest Reuse (yes/no)	Date ended, Day of nesting cycle the nest ended	0.2981
4	Nest Reuse (yes/no)	Rodent SCU relative abundance, Avian SCU relative abundance	0.0680
5	Nest Reuse (yes/no)	Avian SCU relative abundance	0.0578
7	Avian SCU presence	Reduced-dimensionality vegetation variables (Clusters 1,2,3)	0.1888
8	Avian SCU presence	Date ended, Day of nesting cycle the nest ended	0.1353
9	Avian SCU presence	Avian SCU relative abundance, Parent PCE presence	0.1427
10	Avian SCU presence	Avian SCU relative abundance	0.0775
11	Rodent SCU presence	Reduced-dimensionality vegetation variables (Clusters 1,2,3)	0.6249
12	Rodent SCU presence	Date ended, Day of nesting cycle the nest ended	0.1906
13	Rodent SCU presence	Rodent SCU relative abundance, Parent PCE presence	0.7616
Objective 2			
14	Parent PCE presence	Reduced-dimensionality vegetation variables (Clusters 1,2,3)	0.3057
15	Parent PCE presence	Avian SCU presence, Rodent SCU presence	0.4161
16	Parent PCE presence	Avian SCU relative abundance, Rodent SCU relative abundance	0.6052
17	Parent response (number of times chased/number of visits to the nest)	Guild type (Avian SCU, Rodent SCU, Predator, Non-parent PCE), Nest ID (random effect)	0.0126

Objective 2. We used generalized linear regression models to test if parent PCE presence at the nest was affected by vegetation, behavioral, seasonal, and count explanatory variables (Table 3-1, Models 14-16 in Table 3-2).

We tested if parent PCEs responded to the presence of other PCEs, avian SCUs and rodent SCUs using a generalized linear mixed model, with parent response (number of times a species was chased divided by the number of times it visited the nest)as the response variable with a binomial distribution and the type of species being chased (avian SCU, rodent SCU, predator, other PCEs) as the explanatory variable (Table 3-1, Model 17 in Table 3-2). Nest ID was included as a random effect (PROC GLIMMIX, SAS Institute 2015).

We considered models to perform better than a null model if their overall model p-value < 0.05. We considered parameter estimates to be significant if $\alpha < 0.05$ or if odds ratio 95% confidence intervals overlapped 1. We report parameter estimates for models with $P < 0.07$. We used separate models to avoid over-fitting our small sample size with too many parameters. All analyses were conducted using SAS/IML 14.1 software (SAS Institute 2015) and R 3.4.0 (R Core Team 2017).

RESULTS

Nest Outcomes

We monitored four Hairy Woodpecker nests, four Northern Flicker nests, eight Black-backed Woodpecker nests, and fifteen White-headed Woodpecker nests for a total of thirty-one nests. However, we only obtained useable video data for twenty-two of the nests, for a total of 1,093 hours of video footage. Students watched 182 hours (16.6%) of this video.

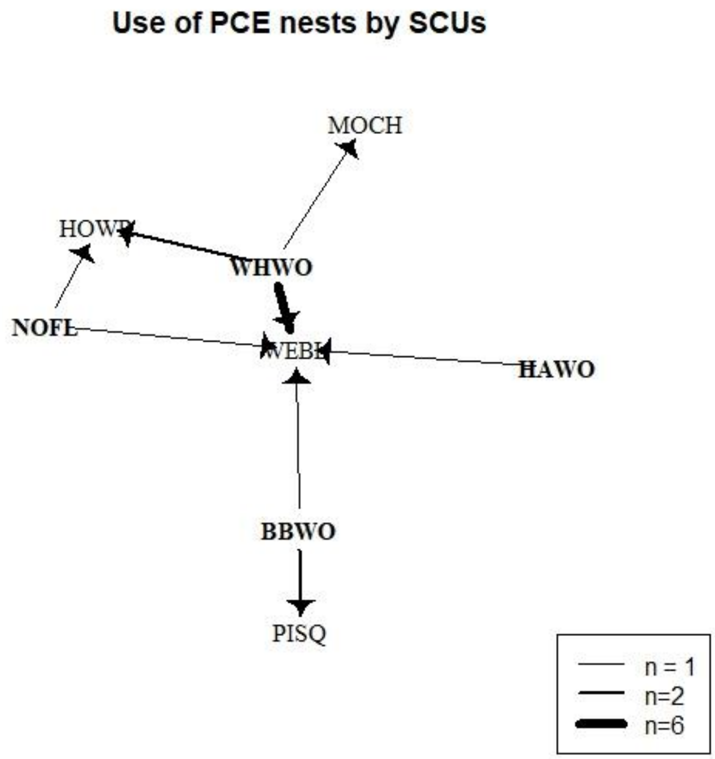
One Northern Flicker nest was abandoned during incubation, and nine White-headed Woodpecker nests failed. Three White-headed Woodpecker nests successfully raised only one chick, with the others dying in the nest. One White-headed Woodpecker nest failed for unknown reasons (heavy fog covered the camera), but two chicks were found dead in the cavity. One Black-backed Woodpecker pair was shot, and their nest was re-used by a second Black-headed Woodpecker pair (Table 3-3, Lorenz et al. 2018).

Table 3-3: PCE nest outcomes in Central Washington in 2016.

Species	Total no. of nests monitored	No. of successful nests	No. of failed nests	Reasons for failure (if applicable)
Hairy Woodpecker	4	4	0	NA
Northern Flicker	4	3	1	Abandoned during incubation
Black-backed Woodpecker	8	8	*1	Parents shot during excavation. *Reused later by another Black-backed Woodpecker pair that successfully fledged chicks.
White-headed Woodpecker	15	6	9	7 nests: Unknown 2 nests: Depredated (American Kestrel, Long-tailed Weasel).

Fourteen out of thirty-one nests were reused by rodent or avian SCUs in the 2016 breeding season. The most common SCUs we detected in our counts were Western Bluebird (*Sialia mexicana*), House Wren (*Troglodytes aedon*), Mountain Chickadee (*Poecile gambeli*), Douglas Squirrel (*Tamiasciurus douglasii*), and chipmunks (*Tamias spp.*). Eight nests were reused by Western Bluebirds; two nests by House Wrens, two nests by pine squirrels, and one nest by Mountain Chickadees. One nest was reused by bluebirds and then by wrens (Figure 3-1).

Figure 3-1: Nest web structure between PCEs and SCUs in central Washington in 2016 (n = 31 nests). PCEs are bolded, SCUs are not bolded. Edge weight indicates how many times any SCU used the nest of that PCE. WHWO = White-headed Woodpecker, BBWO = Black-backed Woodpecker, HAWO = Hairy Woodpecker, NOFL = Northern Flicker, PISQ = Pine squirrel (Douglas squirrel), HOWR = House Wren, WEBL = Western Bluebird, MOCH = Mountain Chickadee.



Nest Reuse and SCU Presence

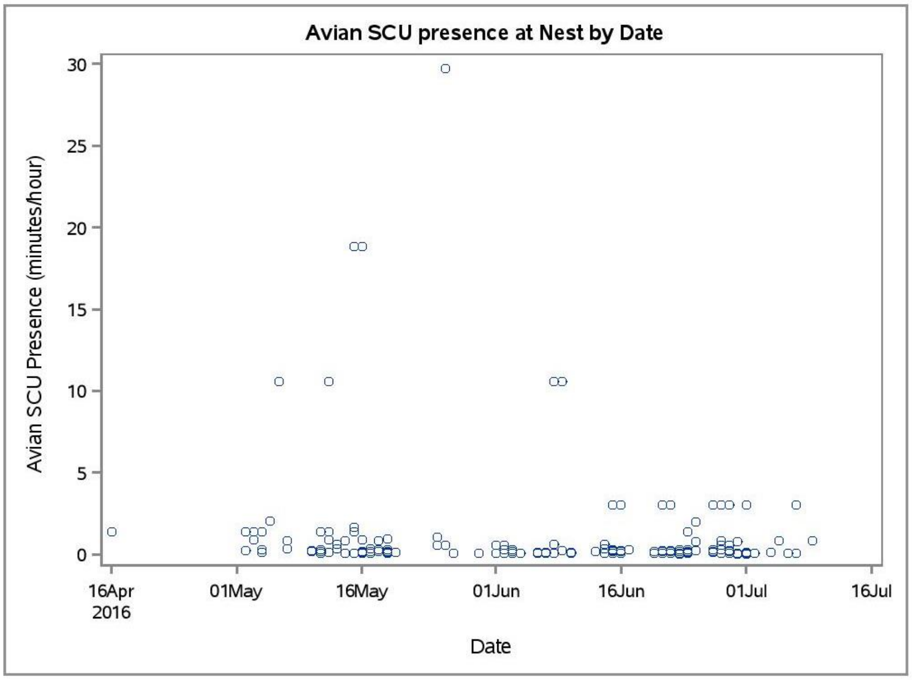
No vegetation, behavioral, seasonal, or count models with multiple variables significantly predicted nest reuse by SCUs (Table 3-2). However, a model containing only avian SCU counts as an explanatory variable was nearly significant, with a parameter estimate that was positive and thus suggest a positive trend with nest reuse (Model 5 in Table 3-2, Table 3-4).

Table 3-4: Parameters estimates +/- SE, with odds ratios from the model predicting PCE nest reuse by SCUs in central Washington in 2016 with only avian SCU counts.

Analysis of Maximum Likelihood Estimates					
Parameter	**Degrees of Freedom**	**Estimate**	**Standard Error**	**Wald Chi-Square**	**P > |F|**
Intercept	1	-2.3195	1.3721	2.8579	0.0909
Avian SCU count	1	0.5184	0.3072	2.8484	0.0915
Odds Ratio Estimates					
Effect		**Point Estimate**	**95% Wald Confidence Limits**		
Avian SCU count		1.679	0.920	3.066	

No vegetation, behavioral, seasonal, or count models with multiple variables had a significant relationship with avian SCU presence at the nest. One model containing only avian SCU counts as an explanatory variable demonstrated a nearly significant relationship with avian SCU presence at the nest (Model 10 in Table 3-2, parameter estimate = 0.009, p = 0.0775). Cluster 1 had a significant relationship with avian SCU presence at the nest (parameter estimate = 0.00771, p = 0.0374), even though the probability for the entire model was not significant ($F_{d.f. = 3}$ = 1.81, p = 0.1888). No models significantly predicted rodent SCU presence at the nest. The highest presence of avian SCUs at nests occurred during the month of May (Figure 3-2).

Figure 3-2: Presence of avian SCUs at PCE nests in central Washington in 2016 (total duration of visits (in minutes) per 2-hour video segment) by date (n = 22 nests).



Parent PCE presence and Defensive Response

No vegetation, behavioral, seasonal, or count models contained significant relationships with parent PCE presence at the nest (Table 3-2). Avian SCUs visited active PCE nests more often than rodent SCUs, predators, or non-parent PCEs, but they were chased less often ($F_{d.f. = 3}$ = 4.46, p = 0.0126, Table 3-5).

Table 3-5: Visits and number of chases by parent PCEs by guild category for PCE nest in central Washington in 2016. All nests are combined.

Species	No. of visits w/ chases	No. of visits w/out chases	No. of total visits
Avian SCU	8	193	201
Rodent SCU	5	27	32
Predators	5	13	18
Other PCEs	6	16	22

DISCUSSION

Almost half of the PCE nests in our study were reused in the same season by avian SCUs and rodents. While many studies have documented nest reuse (Aitken et al. 2002, Martin et al. 2004, Saab et al. 2004, Tarbill et al. 2015), to our knowledge, there appear to be no studies that directly examine nest reuse within the same breeding season in western coniferous forests. Nest reuse rates of PCE cavities between seasons is highly variable among studies, ranging from 86% (Tarbill et al. 2015) to 28% (Aitken et al. 2002). Out of the fourteen nests that were reused in our study, three nests were reused within the month of May, nine in June, and two nests during July. PCEs nesting earlier in the breeding season may face increased pressure from SCUs (Wiebe 2003), and we did find that avian SCU presence at nests peaked during the month of May. However, it appears that demand for nests by SCUs is present throughout the entire duration of the breeding season.

While usurpation of PCE nests by Western Bluebirds has been documented in our study area before (Cowell et al. 2017), no such negative interactions occurred in the 2016 breeding season. In fact, the presence of nesting Western Bluebirds may at times be beneficial for nesting PCEs. One bluebird pair nesting in a Hairy Woodpecker cavity from the 2015 breeding season were seen chasing a chipmunk away from a nearby Northern Flicker nest and other bluebirds away from another Hairy Woodpecker nest.

We failed to find significant models to explain nest reuse, our first study objective. Only one variable approached significance: avian SCU counts. Avian SCUs are important players in the nest web dynamics of our study area. Thus, models with only avian SCU variables may prove to be more predictive. Douglas squirrels were the only rodent species to reuse PCE nests in our study. The more common chipmunk species are not obligate cavity nesters (Broadbrooks 1974) and were not detected using nests. Landscape level vegetation variables, which were not a part of this study, may have greater predictive power than the nest site variables we measured (Saab et al 2004).

We found anecdotal evidence for nest competition among SCUs. At one Hairy Woodpecker nest finished on May 26, a pair of Western Bluebirds occupied the nest four minutes after the last nestling fledged. At a Black-backed Woodpecker nest, a pine squirrel was seen on the nest tree five days before the last nestling fledged. It occupied the nest with 24 hours of fledging. Both these events occurred in an area that burned in 2015. Other nests that have been usurped in our study area were in recent burns (Cowell et al. 2017). Limited variability in the fire history of our nests prevented more in-depth analysis, but we believe it is important to further understand how fire influences nest competition, and consequently SCU behavior (Saab et al. 2004).

We also failed to find significant models to explain the response of PCEs to other individuals at the nest site, our second objective. Parental presence was not significantly predicted by SCU presence or density. Rodents rarely visited nests in the video footage, and avian SCUs cautiously investigating a cavity may not be detected by parent PCEs.

Few studies have provided more than anecdotal evidence for active PCE defense in western coniferous forests (Paclik et al. 2009, but see Vierling 1998). Overall, chase events were rare in the footage we reviewed, but we documented parent PCEs defending nests by physically blocking the entrance to the nesting cavity, lunging out at other animals from within the cavity, performing an open-wing display (Kilham 1962, Ligon 1970) when outside of the cavity, and physically flying at animals outside of the cavity.

Relationships in these nest webs may also influence the probability of predation on PCE nests. Predators may learn cues from other animals visiting the nest (Pelech et al. 2010). In other avian nesting guilds, nests sites that are used by multiple species are exposed to greater risks of predation because of an increase in prey density (Martin 1993). Predators may also learn from other predators. After the male White-headed Woodpecker defended the nest against a Stellar's Jay, an American Kestrel (*Falco sparverius*) depredated the nest six hours later. It is still unknown whether predators learn of active cavities from watching other predators.

Nest web relationships may also help cavity nesters cooperatively defend nests against common predators. When a Long-tailed Weasel (*Mustela frenata*) appeared at a White-headed Woodpecker nest, a Northern Flicker was seen chasing the weasel along with the male White-headed Woodpecker. Mobbing a common predator benefits all nests in an area (Flasskamp1994) Jackdaws (*Corvus monedula*) nesting in old PCE cavities, experienced reduced predation from Pine Martens (*Mattes mattes*) by breeding in larger colonies (Johnsson 1994). Thus, nesting closer to other PCEs and SCUs may be beneficial for nesting PCEs in defending nests from predators.

A goal of the larger study was to determine if rodents were reducing nesting success in woodpecker populations in our study area by preying on eggs and nestlings. Out of the twenty-two nests for which we had a definitive outcome, there was no evidence of rodent predation. Our definitive predator identifications included an American Kestrel and a long-tailed weasel. While we can confirm that while rodents did visit cavities, they did not depredate any of the nests in our study.

Reviews of PCE nesting behavior have expressed the need for studies using continuous video surveillance to provide evidence on PCE nest defense, predation, and nest competition (Paclik et al. 2009). Video surveillance is the most accurate method for identifying other avian nest predators (Thompson 2007, Weidinger 2008), and through the use of continuous surveillance, we were able to provide detailed descriptions of parental, avian SCU, rodent, and predator behavior around PCE nests unachieved by other studies. Our study was limited by sample size, thus, we recommend future studies focus on larger samples of specific species across the entirety of a nesting season in order to create accurate depictions of the relationships within these nest webs and how they influence nesting success.

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Author Contributions:

S.D.C. and K.A.S. conceived the idea, design, experiment, performed the experiments, wrote the paper, developed or designed methods, and analyzed the data; T.J.L and P.C.F. Conceived the idea, design, experiment, performed the experiments, developed or designed methods, and contributed substantial materials.

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APPENDICES

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