THESIS

OUT WITH THE OLD AND IN WITH THE NEW? INVESTIGATING COMPETITION BETWEEN BARRED OWLS (S*TRIX VARIA*) AND NORTHERN SPOTTED OWLS (*STRIX OCCIDENTALIS CAURINA*) IN NORTHWESTERN CALIFORNIA WITH A PLAYBACK EXPERIMENT

Submitted by
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WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY NICHOLAS J. VAN LANEN ENTITLED OUT WITH THE OLD AND IN WITH THE NEW? INVESTIGATING COMPETITION BETWEEN BARRED OWLS (S*TRIX VARIA*) AND NORTHERN SPOTTED OWLS (*STRIX OCCIDENTALIS CAURINA*) WITH A PLAYBACK EXPERIMENT BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

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ABSTRACT OF THESIS

OUT WITH THE OLD AND IN WITH THE NEW? INVESTIGATING COMPETITION BETWEEN BARRED OWLS (S*TRIX VARIA*) AND NORTHERN SPOTTED OWLS (*STRIX OCCIDENTALIS CAURINA*) IN NORTHWESTERN CALIFORNIA WITH A PLAYBACK EXPERIMENT

The Northern Spotted Owl (*Strix occidentalis caurina*) is a controversial species in the Pacific Northwest that is listed as threatened under the Endangered Species Act. The Barred Owl (*Strix varia*), a species historically restricted to eastern North America, has recently expanded its range to completely overlap that of the Northern Spotted Owl. Recent evidence suggests that Barred Owls may displace Northern Spotted Owls from their territories. The focus of my study was to determine whether Barred Owls have the potential to competitively exclude Northern Spotted Owls from their territories. I used a playback experiment to observe and quantify aggressive vocal and physical behavior of Barred and Northern Spotted Owls during territorial defense. Trials consisted of displaying a Northern Spotted or Barred Owl taxidermy mount, and broadcasting recorded vocalizations of the corresponding species, in both Barred and Northern Spotted Owl territories. The frequency and intensity of residents' responses to playbacks were digitally recorded as was the acceleration experienced by the mount's head during physical attacks by the residents.

When agonistic interspecific interactions occurred in this study I found that Barred Owls responded with higher levels of vocal and physical aggression than Northern Spotted Owls. However, the frequency of interspecific interactions was lower compared to intraspecific interactions among Northern Spotted Owls alone. This study suggests that Barred Owls are likely to assume the dominant role during interspecific interactions with Northern Spotted Owls and indicates that competitive exclusion is a plausible mechanism by which Barred Owls could contribute to the observed population declines of Northern Spotted Owls in areas of co-occurrence.

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CHAPTER 1

TERRITORIAL VOCAL BEHAVIOR OF BARRED AND NORTHERN SPOTTED OWLS IN NORTHWESTERN CALIFORNIA

INTRODUCTION

The Northern Spotted Owl (S*trix occidentalis caurina*) was listed as a threatened species in 1990 under the Endangered Species Act due to observed population declines throughout its range (U.S. Fish and Wildlife Service 1990). Because of this species' close association with mature and old-growth coniferous forest (Forsman et al. 1984), early conservation efforts focused primarily on preserving older forests. Continued declines of Northern Spotted Owl populations have been observed despite the development and implementation of the Northwest Forest Plan (Anthony et al. 2006), which was designed to better control levels of timber harvest. Although habitat loss remains a concern for the long-term conservation of the Northern Spotted Owl, the recent range expansion of the Barred Owl (*Strix varia*), a potential competitor, into the range of the Northern Spotted Owl has been identified as another important threat (Taylor and Forsman 1976, Hamer et al. 1994, Kelly et al. 2003, Anthony et al. 2006, Buchanan et al. 2007, Gutiérrez et al. 2007).

Although the Barred Owl was historically absent from western North America, its range has expanded westward over the last eighty years (Grant 1966, Mazur and James 2000, Noon and Blakesley 2006, Buchanan et al. 2007). Barred owls were first reported within the Northern Spotted Owl's range in British Columbia in 1969 (Stirling 1970), and quickly moved south through Washington, Oregon, reaching California by 1981 (Evens and LeValley 1982). Although Barred Owls are now found throughout the Northern Spotted Owl's range (Buchanan et al. 2007), the potential large-scale impact of Barred Owls on Northern Spotted Owls varies considerably across different portions of the Northern Spotted Owl's range. In 2006, Barred Owls occupied as many as 50% of historic Northern Spotted Owl territories in parts of Washington while only occupying approximately 15% of historic Northern Spotted Owl territories in northern California (Anthony et al. 2006, Franklin et al. 2009).

Numerous studies have investigated the influence of Barred Owls on Northern Spotted Owl survival, fecundity, and territory occupancy (Kelly et al. 2003, Olson et al. 2005, Anthony et al. 2006) to better understand the effects Barred Owls may have on components of Northern Spotted Owl fitness. As Barred and Northern Spotted Owls are closely related, a situation typically leading to severe interspecific competition (Lack 1946), the slightly larger Barred Owl is thought to outcompete and displace the Northern Spotted Owl. Supporting this idea, Northern Spotted Owl territory occupancy declined when Barred Owls were detected within 800m of Northern Spotted Owl territory centers (Kelly et al. 2003) and local extinction rates of Northern Spotted Owls from territories increased while colonization rates decreased when Barred Owls were present (Olson et al. 2005). Rates of Northern Spotted Owl vocal responses to surveys also declined in the presence of Barred Owls (Crozier et al. 2006). Collectively, these studies suggest that interspecific competition between these two species is a plausible explanation for reduced Northern Spotted Owl populations in areas of suitable habitat when Barred Owls are also present (Livezey and Fleming 2007).

Interspecific competition can be expressed as exploitative or interference competition (Pianka 1994). Exploitative competition arises from individuals competing over resources, such as nest sites or food, and results in an indirect reduction in survival and/or fecundity for one or both of the species involved. In contrast, interference competition takes the form of direct and aggressive interactions between individuals, occasionally culminating in physical altercations or even mortality.

Under exploitative competition, increased pressure exerted on a prey base shared by two coexisting species can typically reduce overall prey density in an area. This reduction of prey often results in lower rates of fecundity and survival for one or both species (Morin 1999). Although Barred and Northern Spotted Owl territories share many similarities, little overlap exists in diet composition of the two species (Mazur and James 2000, Hamer et al. 2001, Forsman 2004). Additionally, Anthony et al. (2006) found little effect of Barred Owl presence on Northern Spotted Owl fecundity, but they did observe a decline in survival in some populations of Northern Spotted Owls when Barred Owls were present. Given little diet overlap between these species, it seems more likely that declines in Northern Spotted Owl survival could be a result of direct interactions between the two species rather than exploitative competition.

In interference competition by territorial species, aggressive defense of territories encompasses both territorial vocalizations and direct physical aggression. Previous studies have demonstrated that Barred Owls readily respond to Northern Spotted Owl territorial calls (Dunbar et al. 1991, Herter and Hicks 2000), and anecdotal evidence suggests that Barred Owls may prey upon Northern Spotted Owls (Leskiw and Guiterrez 1998). Furthermore, the most extreme form of interference competition, intraguild predation, is largely influenced by body size and level of trophic specialization (Polis et al. 1989). Generally, larger species with broader diets are more likely to engage in intraguild predation because they are less likely to become injured during the predation event and can benefit from the consumption of the competitor. As a generalist and the larger of the two species, the Barred Owl is expected to engage in this form of interference competition more frequently than the Northern Spotted Owl. Thus, past studies on Northern Spotted and Barred Owl interactions and general theory suggest that interference competition could be a mechanism leading to apparent declines in Northern Spotted Owl survival and occupancy in the presence of Barred Owls.

To date, no study has gauged the level of behavioral aggression displayed between these two species when they come into direct contact. Much of the evidence on interference competition between these species is anecdotal, resulting in a need to quantify this interaction (Kelly et al. 2003, Crozier et al. 2006, Livezey and Fleming 2007). In the present study, I used an experimental approach to investigate the behavioral interactions in the defense of territories against both hetero- and conspecifics to assess the magnitude of competitive interactions and to determine whether interference competition can take place when these two species co-occur.

I used playbacks of intra- and interspecific vocalizations to investigate the behavioral interactions between Barred and Northern Spotted Owls because of the important role vocalizations play in Northern Spotted and Barred Owl territory defense (Forsman et al. 1984, Nicholls and Fuller 1987), and the effectiveness of playback experiments in eliciting competitive responses in these, and other, owl species (Trapp 1989, Galeotti 1993, Fuszara and Fuszara 2002, Crozier et al. 2005, Crozier et al. 2006). I also presented life-sized taxidermy owl mounts during playback trials to mimic actual encounters occurring in the wild as closely as possible. Through simulating inter- and intraspecific interactions and by quantifying response rates, response latency, and aggressive call frequency of the two owl species, I attempted to determine whether or not interference competition is a plausible mechanism by which Barred Owls could contribute to current Northern Spotted Owl population declines.

Specifically, I investigated the "exclusion" and "acquiescence" hypotheses to determine whether Barred Owls could displace Northern Spotted Owls from their historic range. Under the "exclusion" hypothesis**,** Barred Owls actively exclude Northern Spotted Owls through interference competition by using frequent and rapid responses coupled with elevated rates of calling when faced with a potential Northern Spotted Owl intruder. Under the "acquiescence" hypothesis, Northern Spotted Owls defend their territories less vigorously against Barred Owls than against other Northern Spotted Owls, as evidenced by lower response rates, increased latency to response, and less frequent calling. To examine both of these hypotheses, I investigated the overall response rate, vocal response latency (i.e., rapidity of vocal response), and frequency of aggressive vocalizations directed at perceived intruders by the resident(s).

METHODS

Study Area

This study took place in four different areas which were concurrently being surveyed for Northern Spotted Owls: Redwood National Park (RNP), Green Diamond Resource Company lands (GDRC), Hoopa Tribal lands (Hoopa), and the Willow Creek study area (WCSA) located within the Six Rivers National Forest. All of these areas are located within Humboldt and Trinity counties in northwestern California (Figure 1.1).

Despite being in close proximity to each other, two distinct vegetative communities exist on the different study areas. RNP and the majority of GDRC lands are located within 32 km of the Pacific coast where redwood (*Sequioia sempervirens*) and Douglas fir (*Pseudotsuga menziesii*) trees are the dominant forest over-story species and the under-story vegetation largely consists of tanoak (*Lithocarpus densiflorus*), California black oak (*Quercus kelloggii*), Oregon white oak (*Q. garryana*), bigleaf maple (*Acer macrophyllum*), red alder (*Alnus rubra*), California bay (*Umbellaria californica*), and madrone (*Arbutusmenziesii*) (Diller and Thome 1999). Due to the close proximity to the coast, these two mesic study sites experience milder temperatures and higher rates of precipitation throughout the year than the Hoopa and WCSA sites (Ting 1998).

The Hoopa and WCSA sites are located directly east of RNP and the GDRC lands, and the coniferous forests in these two study areas lack redwood trees because of the more xeric climate further inland. The over-stories of these two areas are instead dominated by Douglas fir mixed with madrone, and contain a larger proportion of oak woodland forests dominated by tanoak, California black oak, Oregon white oak, and bigleaf maple than the coastal sites (Ting 1998, Franklin et al. 2000).

Owl abundance and species composition are variable across the four study sites. In general, the RNP and Hoopa sites are thought to have a greater proportion of historic Northern Spotted Owl territories occupied by Barred Owls than do the WCSA and GDRC sites. For example, in 2003 Barred Owls were detected at approximately 50% of the historic Northern Spotted Owl territories within RNP (Schmidt 2004) whereas they were detected at fewer than 20% of historic Northern Spotted Owl territories on the WCSA site (Franklin et al. 2009).

Experimental Design

Experimental playback trials were conducted on Barred and Northern Spotted Owl territories in northwestern California from mid-May through mid-August of each year in 2008 and 2009. Territories acted as the sampling unit and were randomly drawn from sampling frames developed for Barred and Northern Spotted Owls, respectively. The study was a quasi-experiment because the species residing within each territory could not be randomly assigned to that territory. Therefore, random assignment was done at the level of playback species presented (Barred or Northern Spotted Owl) for all territories selected from the two sampling frames.

As the sampling unit, territories were defined as 710m radius circles (Franklin et al. 2000) centered on areas where either Barred or Northern Spotted Owls had been detected during the current and preceding breeding seasons or areas where Barred or Northern Spotted Owls were determined to be actively breeding during the current field season. The centers of all Northern Spotted and Barred Owl territories were delineated on each of the four study areas by averaging the Universal Transverse Mercator (UTM) coordinates of detections from the previous seasons for each territory. As territory boundaries change little from year to year (Nicholls 1973, Miller 1974, Forsman et al. 1984), I assumed these circular areas reflected areas actively defended by owls, which reduced the possibility of conducting trials at parts of an owl's home range that were visited infrequently (Forsman et al. 1984). This collection of Northern Spotted and Barred Owl territories represented two separate sampling frames from which territories for experimentation were drawn. Territories to be sampled were chosen randomly from the sampling frame each year, without replacement, to prevent owl habituation to the treatment. In total, 64 and 63 territories were selected for trials conducted in the 2008 and 2009 field seasons, respectively, resulting in a total of 127 trials.

Playback trials for each territory were conducted within 100m of the most recent daytime detection obtained by field crews conducting owl surveys within the current breeding season, provided that it was within the designated territory circle. In instances where no daytime location was available, trials were conducted within 100m of the most recent nighttime detection. In the event that both members of the pair were found at separate locations during the last survey, the trial was conducted within 100m of the male's location because males typically defend territories more actively than females (Forsman et al. 1984, Freeman 1999). For all trials, I attempted to conduct playback trials on ridges to maximize resident owls' detecting the playback, and observers' detecting vocalizations by resident owls.

Trials were conducted under three treatment types consisting of the resident species (Barred or Northern Spotted Owl) occupying the territory and the species (Barred or Northern Spotted Owl) whose vocalization was broadcast within the resident territory. For trials under the first treatment type, I presented a Northern Spotted Owl taxidermy mount and broadcast Northern Spotted Owl vocalizations in a Northern Spotted Owl territory. This treatment type served as a local control and provided baseline data on intraspecific competition occurring among Northern Spotted Owls. Trials in the second treatment type consisted of displaying a Barred Owl mount and broadcasting Barred Owl vocalizations within a Northern Spotted Owl territory to examine aggression levels of Northern Spotted Owls in defending territories from Barred Owls. Trials in the third treatment type consisted of displaying a Northern Spotted Owl mount and broadcasting Northern Spotted Owl vocalizations within a Barred Owl territory to examine aggression levels of Barred Owls in defending their territories against Northern Spotted Owls. Seventeen additional trials in which a Barred Owl resident was presented with the Barred Owl treatment were conducted over the two seasons but were not included in these analyses. Although there are important biological implications of intraspecific competitive interactions between territorial Barred Owls, the goal of my work focused on determining whether competitive interactions with Barred Owls could negatively influence Northern Spotted Owl populations.

For each of two summer field seasons, I initially proposed to conduct experimental trials at 21 territories for each of the 3 treatment types (Table 1.1). To control for seasonal effects on territoriality (Reid et al. 1999, Waldo 2002), I assigned trials for all three treatment types evenly across the seasonal periods. Due to logistic constraints, such as weather complications and a shortage of known Barred Owl territories, the actual sampling of treatment groups differed slightly from the targeted sample (Table 1.1). Trials were only conducted under conditions consistent with current Northern Spotted Owl monitoring protocols (Forsman 1983) to maximize detection of owls during trials, such as not conducting trials when wind speeds exceeded 12 mph, during precipitation, or when heavy fog limited visibility to <50 meters.

Playback Procedures

Northern Spotted and Barred Owls are most active shortly after sunset (Forsman et al. 1984, Brewster and Chapman 1891). In order to conduct the trials when resident owls were active, but still near their roost sites, all trials began 30−60 minutes after official sunset time (NOAA Earth System Research Laboratory 2008).

I used taxidermy mounts from salvaged Northern Spotted and Barred Owl carcasses. These mounts were constructed of a firm Styrofoam interior covered by Northern Spotted or Barred Owl study skins complete with feathers. For each trial, the base of the appropriate taxidermy mount was directly attached on top of an amplifying speaker. The owl mount and speaker were oriented to broadcast sound in the direction the mount was facing. Together, the mount and speaker were affixed atop a 1.5m tall, 3cm diameter aluminum pole, which was secured by placing it onto a 61cm length of rebar that was driven halfway into the ground and stabilized using guide wires. I rotated the direction of the speaker and mount by pulling on a rope attached to the pole on which the owl mount was perched. The mount was initially set up facing an arbitrarily chosen direction (typically down slope), and then rotated ninety degrees at five minute intervals following the start of the playback, resulting in three full revolutions during each trial. By rotating the direction that the speaker and taxidermy mount were facing, I was able to broadcast vocalizations in all directions to increase the chances that the treatment was detected by the resident owls. Additionally, a moving owl mount was thought to more closely mimic a live owl while increasing the visibility of the mount to any approaching residents.

Recorded vocalizations were played using a continuous compact disc (CD) recording lasting 60 minutes. Each playback recording contained five periods of intermittent calling separated by approximately four-minute periods of silence. The composition of call types within the calling periods changed throughout the duration of the playback CD (Table 1.2) to simulate an intruder becoming increasingly agitated. Male vocalizations were used in both recordings because males of both species are more likely to vocalize in territorial defense (Forsman et al. 1984, Freeman 1999). The chosen vocalization frequencies mimic Northern Spotted Owl and Barred Owl vocalization delivery in the wild (Forsman et al. 1984, Johnson 1993, Mazur and James 2000).

Data Collection

At the start of each trial the following data were recorded: treatment species, resident species, names of all observers present, UTM coordinates of the trial location, resident owl species, elevation of the trial location, time the playback was started, ambient temperature (ºF) using a portable thermometer, wind speed measured with an anemometer, and visible moon phase (coded as quarter from 0 through 4; Franklin et al.

1986). Upon the start of the playback, between 1 and 3 observers concealed themselves 15–20m from the owl mount and remained quiet for the duration of the trial.

In the event of a response, the time, species, sex, approximate distance, and bearing were recorded. Each vocalization produced by a resident owl was documented along with the time and sex of the vocalizing owl. Additionally, an omni-directional microphone with windscreen was used to record the resident pair's vocalizations for data-proofing in the laboratory. Vocalizations of both Northern Spotted and Barred Owls were classified into one of three categories: contact call, territorial call, or aggressive call (Table 1.3) based on descriptions in Brewster and Chapman (1891), Bent (1938), Forsman et al. (1984), and McGarigal and Fraser (1985). Furthermore, detailed field notes describing all behaviors observed were recorded throughout the experiment. During all trials conducted in 2008, one observer was equipped with a set of Rigel 3200 pro night vision goggles (Rigel Optics, Inc., Washougal, WA) to facilitate the detection of owls that silently approached the model. In 2009, two observers were equipped with night vision goggles.

Some playback trials were truncated for one of two reasons. On occasion, the responding individuals struck the owl mount with sufficient force to dislodge it such that it could not be re-attached. For these cases the trial was truncated at the time of the strike. The second reason for truncating trials was much more common and resulted from neighboring hetero- or conspecifics responding to either the playback treatment or to the vocalizing residents. In these instances, the response of the residents could no longer be attributed strictly to the presented playback treatment, so trials were truncated when the neighbor first vocalized. At the conclusion of each trial, the time the trial concluded, the temperature, wind speed, moon phase, and any additional notes regarding the trial were recorded.

Data Analyses

Competing hypotheses were expressed as statistical models where detection of a response (yes or no), latency to first vocalization, and aggressive call frequency were the modeled response variables (Table 1.4). Response variables were tabulated and the analysis was conducted separately for the male resident, female resident, and the territory (i.e., a response was recorded on the territory from the male, the female, or both). For all model sets, the treatment type (*TT*) (the combinations of the playback species presented and the resident species) was included as an explanatory variable.

Statistical models were analyzed with the experimental data using SAS software (SAS Institute 2003). PROC LOGISTIC was used for logistic regression analyses to examine the general responsiveness of residents (i.e., whether they responded or not to the treatment), and PROC GENMOD was used for linear regressions examining continuous response variables describing the magnitude of responses (i.e., vocal response latency and aggressive call frequency).

Additional variables were included in the models as covariates (Table 1.5) to ensure that variation among treatments was not confounded with other effects. These covariates were considered important because of their potential effects on the rate and intensity of responses. For example, timing within the season has been found to affect territorial behavior of Northern Spotted and Barred Owls (Ganey 1990, Mazur and James 2000, Waldo 2002), lunar cycles can affect Northern Spotted Owl behavior (Ganey

1990), and the duration of occupancy of territories has been shown to affect the ability of individuals to hold territories and to affect the intensity of territorial responses by residents of other avian species (Hyman et al. 2004 and Sergio et al. 2009). Additionally, it seems reasonable that resident breeding status, differences in habitat composition, prey base, and amount of time Barred Owls have been recorded as present at the different study sites may all influence overall competition intensity. Because vocal response latency was less than 60 minutes for all truncated trials ($n = 19$), the truncation code was included in all models predicting vocal response latency.

Analytical Strategy

I created three analyses sets to analyze territorial behavior across treatments. The first data set included data from all trials and accounted for both the magnitude and frequency of resident responses to the treatment. The second analysis set consisted of the subset of the data including only trials in which a resident response was detected, and investigated the magnitude of residents' responses when agonistic interactions occurred. Analyses with these subsetted data were considered particularly important because instances in which the residents did not respond as a result of their not detecting the treatment would not impact the results. The third analysis set consisted of trials for which the number of years the resident had occupied the territory was known. Analyses with this data set accounted for the potential impact that duration of territory occupancy could have on the magnitude of territorial responses.

The analyses performed with the all-inclusive data set incorporated data from 126 of the 127 playback trials conducted; one trial was removed from the data set because an owl had been found dead on the road close to the territory, making it unclear whether both resident owls were available for response when the trial was conducted. Separate analyses were conducted for each response variable and at each response level within the territory (male, female, and territory) resulting in nine model sets (Table 1.4).

I used the same set of models as in the all inclusive analyses for analyses conducted with the second analysis set containing data from only trials in which a response was detected. The subsets incorporated data from 79, 49, and 86 trials in which a male, female, or territory response was detected, respectively. Analyses were conducted for the aggressive call frequency and vocal response latency response variables at each level within the territory (i.e., male, female, and territory) resulting in six additional model sets.

The third data set included data for trials conducted at Northern Spotted Owl territories for which the number of years the male (n = 84) or female (n = 80) residents had occupied the territory was known (based on data from marked individuals). I re-analyzed the statistical models where aggressive call frequency was the response variable for all treatment types but included the number of years the individual had spent on the territory as an additional covariate along with additional two- and three-way interactions of interest. Analyses were conducted at the level of the male resident and female resident resulting in two additional model sets. Information regarding the number of years Barred Owls had occupied their territories was unavailable so similar analyses of trials with Barred Owl residents were not conducted.

Model Ranking and Multimodel Inference

An information-theoretic approach was used for all analyses (Burnham and Anderson 2002) to select appropriate models for inference. Models resulting in quasicomplete separation in the logistic regression analyses (SAS Institute 2003) were removed from the model set due to poor model convergence. I ranked the models in each model set using a bias-corrected form of Akaike's Information Criterion (AICc) because of limited sample size (n varied from 49 to 126 for the different model sets). Akaike weights were calculated for each model as the likelihood that a given model in the candidate model set was the best predictive model given the data and the model set.

A priori models in each model set included the treatment effect as well as additive effects of the covariates and two- and three-way interactions which were thought to be biologically meaningful. I computed R^2 values as a measure describing the proportion of variance explained by the models. In the logistic regression models, I used maximum re-scaled R^2 (SAS Institute 2003) and in the linear regression models I used values from PROC GLM in SAS as an approximation of R^2. For some model sets, additional models were constructed *a posteriori*. These models included additional combinations of additive effects and two-way interactions that held low ΔAICc values during the *a priori* analyses. *A priori* and *a posteriori* models were clearly delineated from each other in the model selection results.

For all model sets, I estimated the parameter for the effect of each treatment type (*TT*), its standard error, and 95% confidence intervals using model-averaging (Burnham and Anderson 2002). In some cases, important covariates were also model-averaged. I felt this was the most appropriate way to assess the influence of variables on resident responses because most model sets contained competing models with non-trivial Akaike weights. The model-averaged parameter estimates for all variables of interest were calculated by normalizing the Akaike weights such that summed Akaike weights among the models containing the variable being assessed were equal to one.

Effects were estimated for treatments where Barred Owl residents were presented with the Northern Spotted Owl mount and playback treatment and where Northern Spotted Owl residents were presented with the Barred Owl mount and playback by setting the treatment where Northern Spotted Owl residents received the Northern Spotted Owl treatment as the intercept. I examined predictions of the "exclusion" hypothesis by estimating the difference in the parameter estimates for the intercept and the treatment effect where Barred Owl residents were presented with the Northern Spotted Owl playback treatment. Similarly, the "acquiescence" hypothesis was evaluated by estimating the difference in the parameter estimates for the intercept and the treatment effect where Northern Spotted Owls received the Barred Owl playback treatment.

RESULTS

I utilized data from 126 playback trials conducted during the 2008 (n = 63) and 2009 (n = 63) field seasons for the analyses. Of 42 trials in which the Northern Spotted Owl treatment was presented to Northern Spotted Owl residents, there were 8 trials in which no response was detected, 2 trials in which only a female response was detected, 15 trials in which only a male response was detected, and 17 trials in which both male and female responses were detected. I conducted 45 trials where I presented the Barred Owl treatment to Northern Spotted Owl residents. In these 45 trials, I detected no response 13 times, a response by only the female resident 3 times, only a male response 11 times, and both male and female responses 18 times. Northern Spotted Owl playback trials were conducted in 39 Barred Owl territories. Twenty of these trials received no response, 1 trial resulted in only a female response, 10 trials resulted in only a male response, and both the male and female responded in 8 trials.

A larger proportion of trials conducted at Northern Spotted Owl territories were set-up within 100m of a last known location obtained during the daylight hours. Of 87 playback trials conducted at Northern Spotted Owl territories, only 14 (17%) were held at locations obtained between 9:00 PM and 4:00 AM PST. In comparison, 13 of 39 trials (33%) held within Barred Owl territories were conducted at locations obtained by field crews at night. The proclivity for Northern Spotted Owls to approach and perch within sight of the taxidermy mount prior to the initiation of the trial resulted in 26 of 87 (30%) total trials starting with one or more Northern Spotted Owls present. In contrast, 0 of the 37 trials conducted within Barred Owl territories began with a resident in sight. Due to the likelihood that Northern Spotted Owls approached the researchers because of a greater propensity to investigate intruders, data from all trials were incorporated in the analysis despite the potential bias regarding vocal response latency and aggressive call frequency from Northern Spotted Owls.

Overall Response (Response Code)

Data from 126 trials were used in the logistic regression analyses to assess overall responsiveness (i.e., whether a response was detected or not) between Barred and Northern Spotted Owls at the level of male, female, and territory responses relative to intraspecific responsiveness among Northern Spotted Owls.

The top-ranked model for male response was heavily weighted and was almost six times more likely than the second-ranked model (Table 1.6). Together, these two models accounted for all of the Akaike weight. The only difference between these two models was the presence of an interaction in the second-ranked model (Table 1.6). Both models included whether a female was present during the trial (*FP).* Model-averaged estimates of the *FP* effect indicated a strong positive effect on male responsiveness ($\hat{\bar{\beta}}$ = 1.02, 95% CI = 0.52, 1.51) for all treatments. Based on the 95% confidence intervals, model-averaged estimates of *TT* indicated male Barred Owl residents responded similarly to the Northern Spotted Owl treatment ($\hat{\bar{\beta}}$ = −0.47, 95% CI = −1.09, 0.16; Table 1.7) as male Northern Spotted Owl did to the Barred Owl treatment ($\hat{\bar{\beta}}$ = −0.11, 95% CI = −0.69, 0.48; Table 1.7). The top-ranked model in this analysis accounted for 27% of the variation in the data (Table 1.6).

For female responses, there were two models with an Akaike weight >0.1 (Akaike weight = 0.54 and 0.14), one of which was an *a posteriori* model (Table 1.8). Year (*YC)* and reproductive status (*RC)* were also included in the top-ranked models. The 95% confidence intervals for the model-averaged parameter estimate for *RC* and *YC* suggested that these effects were not strong ($\hat{\bar{\beta}}$ = 0.18, 95% CI = −0.50, 0.85 and $\hat{\bar{\beta}}$ = −0.50, 95% CI = −0.88, −0.11, respectively). Female Barred Owl responsiveness to the Northern Spotted Owl treatment was lower than intraspecific responsiveness among Northern Spotted Owls ($\hat{\bar{\beta}}$ = −0.69, 95% CI = −1.35, −0.02; Table 1.7) with the 95% confidence interval barely overlapping zero. In contrast, female Northern Spotted Owls appeared to respond equally to the Barred and Northern Spotted Owl treatments ($\hat{\bar{\beta}}$ = 0.37, 95% CI =

−0.21, 0.95; Table 1.7). The two top-ranked models in this analysis accounted for 13% and 23% of the variation in the data, respectively (Table 1.8)

Modeling of responsiveness at the territory level did not result in a clear top-model, with no model carrying an Akaike weight >0.25 (Table 1.9). No additional covariates aside from *TT* were repeatedly found among the top models. The model-averaged parameter estimate for *TT* mirrored the results of the female-only response model set listed above, with Barred Owls responding less to the Northern Spotted Owl treatment ($\hat{\bar{\beta}}$ = −0.75, 95% CI = −1.31, −0.20) and Northern Spotted Owls responding similarly to the Barred and Northern Spotted Owl treatments ($\hat{\bar{\beta}}$ = 0.11, 95% CI = −0.45, 0.66; Table 1.7). The top 9 models each explained approximately 10% of the variation within the data (Table 1.9).

Aggressive Calling Frequency

The frequency that individuals aggressively called was modeled with data from a total of 126 playback trials from the male, female, and territory levels. Male aggressive call frequency was strongly influenced by the presence of the female resident, with the models including the *FP* covariate accounting for all of the Akaike weight (Table 1.10). Model-averaging of the *FP* variable effect size suggested that males called more frequently when the female was present ($\hat{\bar{\beta}}$ = 0.95, 95% CI = 0.05, 1.85). Additionally, adjusted Julian date (*AD)* was incorporated in the top three models (combined Akaike weight = 0.83; Table 1.7). However, model-averaged estimates suggested only a weak effect ($\hat{\bar{\beta}}$ = −0.01, 95% CI = −0.14, 0.00). The model-averaged estimate of *TT* for Barred

Owl residents responding to the Northern Spotted Owl treatment indicated they called more frequently in response to Northern Spotted Owls than Northern Spotted Owls did toward conspecifics ($\hat{\bar{\beta}}$ = 0.83, 95% CI = −0.09, 1.75; Table 1.7) with the 95% CI barely overlapping zero. Conversely, Northern Spotted Owl residents responding to the Barred Owl treatment appeared to call less frequently ($\hat{\bar{\beta}}$ = −0.05, 95% CI = −1.00, 0.07; Table 1.7) with the 95% CI narrowly including zero. Top-ranked models in this analysis explained between 18 and 30% of the variation in the data (Table 1.10).

Female calling frequency was potentially influenced by year (*YC)* and reproductive status (*RC)* as these two covariates were each found in two of the top three models (Table 1.11). Model-averaged parameter estimates for *YC* and *RC* indicated that females called more often in 2008 than 2009 and while breeding as opposed to not breeding ($\hat{\bar{\beta}}$ (*YC*) = −0.15, 95% CI = −0.32, 0.03 and $\hat{\bar{\beta}}$ (*RC*) = −0.17, 95% CI = −0.40, 0.05). Female Barred Owl call frequency in response to the Northern Spotted Owl treatment was similar to female Northern Spotted Owl responses to conspecifics ($\hat{\bar{\beta}}$ = 0.05, 95% CI = −0.18, 0.29; Table 1.7). Female Northern Spotted Owls appeared to call more frequently in response to perceived Barred Owl intruders than to other Northern Spotted Owls ($\hat{\bar{\beta}}$ = 0.20, 95% CI = −0.01, 0.42). The top model in this set explained 9% of the variation in the data.

The intercept-only model was the top-ranked model for aggressive call frequency at the territory level indicating an overall lack of a *TT* effect (Table 1.11). Little effect of *TT* was further evidenced by the 95% CI's including zero for both Barred Owls responding to the Northern Spotted Owl treatment ($\hat{\bar{\beta}}$ = 0.00, 95% CI = −0.69, 0.69) and

Northern Spotted Owls responding to the Barred Owl treatment ($\hat{\bar{\beta}} = -0.26$, 95% CI = -1.07, 0.54; Table 1.7). The candidate models explained between 0 and 9% of the variation in the data.

I used a subset of 79 playback trials in which a male responded to estimate the effect of treatment type, *TT*, on male calling frequency, given that a male response was detected. The top model in this set was an *a posteriori* model with covariates from *a priori* models, which included adjusted Julian date (*AD)*, female presence (*FP)* and the interaction of *TT* with *AD* (Akaike weight = 0.73; Table 1.13). The *AD* covariate was incorporated in each of the top seven models (combined Akaike weight = 0.99) and appeared to negatively influence call frequency ($\hat{\bar{\beta}} = -0.02$, 95% CI = -0.03, -0.01) while the *FP* covariate was included in three of the top four models (combined Akaike weight = 0.83) and was positively associated with male call frequency ($\hat{\bar{\beta}} = 0.55$, 95% CI = 0.08, 1.02). Given a response, male Barred Owls called more often when presented with the Northern Spotted Owl treatment than Northern Spotted Owls did when responding to a conspecific ($\hat{\bar{\beta}} = 1.04$, 95% CI = 0.01, 2.08; Table 1.14). In contrast, male Northern Spotted Owls called less frequently in response to the Barred Owl treatment than toward the Northern Spotted Owl treatment ($\hat{\bar{\beta}} = -1.22$; 95% CI of -2.33, -0.11; Table 1.14). Neither 95% CI for the *TT* effect overlapped zero suggesting that calling frequencies differed among the treatments. Models with Akaike weights >0 explained between 20 and 38% of the variation in the data.

A subset of 49 trials was used to estimate female calling frequency, given that a female response was detected during the trial. No single model was particularly useful in predicting female calling frequency with no individual model carrying an Akaike weight

>0.26 (Table 1.15). Model-averaged estimates for *TT* indicated that female Barred Owls responded similarly to the Northern Spotted Owl treatment ($\hat{\bar{\beta}}$ = 0.29, 95% CI = −0.27, 0.84) as female Northern Spotted Owls did to each other. However, female Northern Spotted Owls responded more frequently to the Barred Owl treatment ($\hat{\bar{\beta}}$ = 0.41, 95% CI = −0.03, 0.86; Table 1.14) than they did to conspecifics. The intercept-only model ranked as the second best model, which suggested that the treatment effect was not well supported. Models with Akaike weights >0.05 explained between 0 and 19% of the variation.

Data from 86 trials in which a response by one or more residents was detected were used to analyze aggressive calling frequency at the territory level. Adjusted Julian date (*AD)* was present in the three top-ranked models (cumulative Akaike weight = 0.89; Table 1.16) with a model-averaged estimate ($\hat{\bar{\beta}}$ = −0.02, 95% CI = −0.03, 0.00) suggesting declining call frequencies as the season progressed. Model-averaged estimates of *TT* suggested similar responses by Barred Owls to the Northern Spotted Owl treatment ($\hat{\bar{\beta}}$ = 0.97, 95% CI of −0.30, 2.25; Table 1.14) when compared to Northern Spotted Owl responses to a conspecifics. In addition, Northern Spotted Owls called similarly to the Barred Owl treatment ($\hat{\bar{\beta}}$ = −0.50, 95% CI = −1.86, 0.87; Table 1.14). Models including the *TT* variable explained between 6 and 22% of the variation within these data.

Eighty-four trials conducted at Northern Spotted Owl territories were used to analyze the influence of duration on territory (*MY)* with respect to male aggressive call frequencies. These trials only included data where the number of years the resident male had occupied the territory was known. Model-averaging of *MY* effect size on male calling frequency suggested a slight increase in male calling frequency with increasing duration on territory ($\hat{\hat{\beta}}$ = 0.08; 95% CI = −0.07, 0.23), with the 95% CI barely including zero. However, the magnitude of this effect was small.

Data from 80 trials conducted at Northern Spotted Owl territories, in which the number of years the female had occupied the territory (*FY)* was known, were used to examine the effect that time spent on territory had on female aggressive calling frequency. Models including *FY* had low Akaike weights, with the best model containing *FY* having a weight of 0.09. The effect of *FY* was calculated by averaging the *FY* parameter estimate amongst only the models that contained this covariate, resulting in a $\hat{\hat{\beta}}$ = −0.02 (95% CI = −0.05, 0.02). Models in this set explained only a small amount of variation (range of R^2 = 0.00 – 0.07).

Vocal Response Latency

Vocal response latency was examined using data from 126 playback trials. The female present covariate (*FP)* was included in the top nine models predicting male vocal response latency, with a cumulative Akaike weight = 1.0 (Table 1.19). Although the 95% CI for the model-averaged effect size of *FP* overlapped zero slightly ($\hat{\hat{\beta}}$ = −16.94, 95% CI = −36.19, 2.31), it suggested that males responded quicker during trials in which a female was also detected. Adjusted Julian date (*AD)* was also well-represented in the model set with models containing this covariate totaling an Akaike weight = 0.70. The model-averaged estimate of the *AD* effect size suggested that males responded slightly faster as the season progressed ($\hat{\hat{\beta}}$ = −0.15; 95% CI = −0.33, 0.02). Model-averaged estimates of the treatment effect (*TT)* provided no evidence that Barred Owls responded differently to Northern Spotted Owls ($\hat{\bar{\beta}}$ = 7.00, 95% CI = −9.71, 23.71; Table 1.7) or that Northern Spotted Owls responded differently to Barred Owls than Northern Spotted Owls did to conspecifics ($\hat{\bar{\beta}}$ = −1.14, 95% CI = −13.43, 10.60; Table 1.7). The top-ranked model explained 29% of the variation (Table 1.19).

The top two models predicting female vocal response latency included the year code (*YC*) covariate and had a combined Akaike weight = 0.57 (Table 1.20). The model-averaged estimate of *YC* suggested that females responded more quickly in 2008 than in 2009 ($\hat{\bar{\beta}}$ = 8.56, 95% CI = 0.63, 16.48). Female vocal response latency was longer for Barred Owls responding to the Northern Spotted Owl treatment ($\hat{\bar{\beta}}$ = 15.78, 95% CI of 5.58, 25.98; Table 1.7). No difference was found in female Northern Spotted Owl vocal response latency between trials in which the Barred or Northern Spotted Owl treatment was presented ($\hat{\bar{\beta}}$ = 0.88, 95% CI of −9.19, 10.96; Table 1.7). The percent of variation in these data explained by models including the *TT* variable ranged from 14% to 31% (Table 1.20).

Vocal response latency analyzed at the territory level resulted in all models except the intercept-only model having some Akaike weight, and no model having a weight >0.24 (Table 1.21). No variable aside from *TT* appeared to influence vocal response latency at the territory level. Model-averaged estimates of *TT* suggested that Barred Owls responded more slowly than Northern Spotted Owls did to the Northern Spotted Owl treatment ($\hat{\bar{\beta}}$ = 22.42, 95% CI of 11.94, 32.89; Table 1.7). Northern Spotted Owl residents responded similarly to the Barred and Northern Spotted Owl treatments ($\hat{\bar{\beta}}$ =

2.57, 95% CI of −8.05, 13.18). Models having an Akaike weight >0 explained between 18 and 25% of the variation within the data (Table 1.21).

I analyzed a subset of 79 trials where male residents responded to differentiate vocal response latency among the treatments. All models predicting male response latency had some Akaike weight with no model holding more than 0.21 of the weight (Table 1.22). No variable aside from *TT* and truncation code (*TC*) appeared repeatedly among the top models. Barred Owls responded similarly to the Northern Spotted Owl treatment ($\hat{\bar{\beta}}$ = 7.71, 95% CI = −7.46, 22.88; Table 1.14). Male Northern Spotted Owls appeared to respond more quickly when presented with the Barred Owl treatment as compared to the Northern Spotted Owl treatment with the 95% CI narrowly overlapping zero ($\hat{\bar{\beta}}$ = −5.40, 95% CI of −10.85, 0.05). Models having an Akaike weight >0.01 explained between 21 and 31% of the variation in the data (Table 1.22).

Female vocal response latency was assessed for the 49 trials in which a female response was detected. Model weights were widely distributed across the models tested with only one model receiving no weight and no model receiving an Akaike weight >0.26 (Table 1.23). The number of days between the last known location and the day of the trial (*UD*) appeared in several of the competing models. The model-averaged estimate for *UD* suggested that response latency increased as the number of days between the last known location and the trial increased with the 95% CI overlapping zero slightly ($\hat{\bar{\beta}}$ = 0.12, 95% CI = −0.02, 0.25). Both Barred and Northern Spotted Owl females responded to the interspecific playback treatment similarly compared to Northern Spotted Owls responding to conspecifics ($\hat{\bar{\beta}}$ = 14.93, 95% CI = −21.22, 51.08 and $\hat{\bar{\beta}}$ = 4.99, 95% CI =

−5.71, 15.69 respectively; Table 1.14). Models containing the treatment variable (*TT*) explained 18 – 36% of the variation within the data (Table 1.23).

Vocal response latency at the territory level for trials in which one or more residents responded was analyzed using data collected from 86 trials. Two models had considerably higher Akaike weights than the remaining models and together accounted for >45% of the Akaike weight (Table 1.24). The top model contained the *TT* and *TC* variables while the second-best model incorporated the *TT*, *TC*, and *SC* (Study Code) variables. Model-averaged estimates for *TT* indicated that Barred Owls responded slower than Northern Spotted Owls to the Northern Spotted Owl treatment ($\widehat{\overline{\beta}}$ = 13.67, 95% CI = 7.45, 19.90; Table 1.14). However, Northern Spotted Owls responded similarly to the Barred Owl treatment compared to the Northern Spotted Owl treatment ($\widehat{\overline{\beta}}$ = −2.74, 95% CI = −9.46, 3.99; Table 1.14). Models having an Akaike weight >0 explained between 31 and 40% of the variation in the data (Table 1.24).

Summary of Results

Overall, results provided mixed support for the “exclusion” hypothesis (Table 1.25). The increased frequency of aggressive calling during trials in which a response was detected by Barred Owls compared to Northern Spotted Owls when presented with the Northern Spotted Owl treatment agreed with the hypothesis. However, Barred Owl residents demonstrated lower response frequencies and increased vocal response latencies when receiving the Northern Spotted Owl treatment compared to Northern Spotted Owls, which contradicted my predictions. The results investigating the “acquiescence” hypothesis also provided mixed support (Table 1.25). Overall, the “acquiescence” hypothesis was validated by Northern Spotted Owls calling less frequently when receiving the Barred Owl compared to the Northern Spotted Owl treatment, but similar response frequencies and vocal response latencies between treatments did not meet predictions of the “acquiescence” hypothesis.

DISCUSSION

General Considerations

Broadcasting territorial vocalizations within Northern Spotted and Barred Owl territories resulted in both intra- and interspecific responses by both sexes. In general, male residents responded more frequently than female residents; however, the presence of a female was positively correlated with the magnitude of the male resident’s response. The frequency of responses was higher when conducting playback trials in Northern Spotted Owl territories; however, the intensity of responses by Barred Owls was greater for trials in which a response was detected. These findings indicate that, although interspecific interactions do occur, they are less frequent than intraspecific interactions between Northern Spotted Owls. The higher calling frequency by Barred Owls compared to Northern Spotted Owls when interspecific interactions occurred indicates that Barred Owls are likely to act as dominants during agonistic encounters.

“Acquiescence” Hypothesis

Results of this study demonstrated mixed support for the “acquiescence” hypothesis. I found little difference in overall responsiveness and response latency when

Northern Spotted Owls were presented with the Northern Spotted or Barred Owl playback treatments. These findings failed to support the “acquiescence” hypothesis predicting that Northern Spotted Owls would respond less frequently and more slowly to the Barred Owl treatment compared to their responses to the Northern Spotted Owl treatment. Past experimental work suggested that Northern Spotted Owls were less likely to respond to calls from conspecifics after Barred Owl calls were broadcast in the area (Crozier et al. 2006). Similarly, Olson et al. (2005) and Bailey et al. (2009) found lower detection rates of Northern Spotted Owls in the presence of Barred Owls. Two possible reasons exist for the disparity in past results and the results of this study. First, in the Crozier et al. (2006) study, resident Northern Spotted Owls which received the Barred Owl treatment were presented with Barred Owl calls followed by Northern Spotted Owl calls during each survey whereas their control group was presented with Northern Spotted Owl calls only. The effect they observed may have resulted from residents being less willing to engage in agonistic interactions with multiple “intruders” in an evening instead of Northern Spotted Owls being less vocal in the presence of Barred Owls. A second explanation for the disparity in results is that the duration of Barred Owl occupancy differed among study areas. The studies by Olson et al. (2005) and Bailey et al. (2009) were conducted in Oregon where Barred Owl populations are denser and have been established longer than in northwestern California (Olson et al. 2005). Responsiveness by Northern Spotted Owls in the two Oregon studies therefore, may have differed from that observed in this study due to increased exposure to Barred Owls in the past and subsequent behavioral shifts by Northern Spotted Owls. Supporting the idea that Northern Spotted Owls may exhibit behavioral shifts in the presence of Barred Owls, Crozier et al. (2006) indicated that Northern Spotted Owls responded less often in areas with higher Barred Owl density.

Northern Spotted Owl territories typically show little overlap between pairs (Forsman et al. 1984, Hamer et al. 2007) suggesting that intraspecific competition within Northern Spotted Owls is sufficient to prevent coexistence in a given space. Given that males of both species, which typically assume the primary role in territorial defense, responded with similar frequency and latency among treatments in my study, it appears unlikely that Northern Spotted Owl territories would overlap Barred Owl territories substantially. This idea coincides with recent work which found that significantly more Barred Owl territories were found in unoccupied Northern Spotted Owl territories than in occupied territories (Pearson and Livezey 2003). Past research and my results indicate that Northern Spotted Owls do view Barred Owls as competitors and initiate agonistic interspecific interactions with them, contradicting my "acquiescence" hypothesis.

Smith and Parker (1972) suggested that agonistic encounters are often resolved by asymmetric behavioral or morphological cues, in which one individual demonstrates dominance, without further escalation. In this study, male Northern Spotted Owl aggressive call frequency was lower in trials where they responded to the Barred Owl treatment than in trials where they responded to the Northern Spotted Owl treatment. This indicates a lower magnitude of agonistic behavior by Northern Spotted Owls when faced with the larger Barred Owl and lends support for the "acquiescence" hypothesis (Table 1.25). These results agree with a review of intraguild predation among raptors by Sergio and Hiraldo (2008) in which they found that smaller species will frequently engage in short-term behavioral avoidance, including reduced calling, when faced with larger heterospecifics. Given that males of these two species assume a more prominent role in territorial defense than females (Forsman et al. 1984, Freeman 1999), the asymmetry in response magnitude between Barred and Northern Spotted Owls that I found could indicate that prospecting Barred Owls can overtake Northern Spotted Owl territories by signaling their dominance through frequent and persistent aggressive calls. Although female responses were infrequent, female Northern Spotted Owls responded more vigorously to Barred Owls than to conspecifics. Past research has investigated the potential for reverse size dimorphism to confer advantages in nest defense (Snyder and Wiley 1976, Mueller 1986); however, to my knowledge no study has yet examined effects of reverse sexual size dimorphism on sex-specific roles during territorial defense against larger intruders. As the larger sex, females may exhibit more prominent roles in territorial defense when threatened by larger congeneric intruders with whom they are unfamiliar.

The “Exclusion” Hypothesis

Similar to the “acquiescence” hypothesis, my results provided mixed support for the “exclusion” hypothesis. Interactions between Barred and Northern Spotted Owls occurred less frequently and more slowly than interactions between Northern Spotted Owls alone, which failed to support the “exclusion” hypothesis. Despite general ecological principles which predict that intraspecific competition is generally stronger than interspecific competition (Connell 1983), these results were surprising because of the perception held by researchers that Barred Owls are more aggressive than Northern Spotted Owls (Dark et al. 1998, Herter and Hicks 2000). One element of my study may have contributed to artificially lowering the response rate of Barred Owls. A larger proportion of trials conducted at Northern Spotted Owl territories (84%) were set-up within 100m of a last known location obtained during the daylight hours than trials conducted within Barred Owl territories (66%). It is possible that trials held at daytime roost locations were conducted closer to the center of the resident's territory when compared to locations obtained at night because of both species' propensity to roost at the territory center during daylight hours. This inconsistency in where trials were located within territories could have potentially biased my results because residents may be more likely to detect the treatment and respond when the trial site was closer to the territory center.

Dominance in interspecific interactions can be strongly influenced by body mass between competing owl species (Martínez et al. 2008). My results appear to support this generalization because Barred Owl males that responded to the treatment gave aggressive calls more frequently than the smaller Northern Spotted Owls. More frequent aggressive calling by male Barred Owls may indicate that male Barred Owls dominate during interspecific interactions. Typically, subordinate species mitigate risks from encounters with dominant species through risk-sensitive habitat selection (increasing the proportion of time spent in habitats not occupied by the dominant competitor), distance sensitive avoidance (increasing distance between individuals), behavioral avoidance (reducing vocalizations or actively fleeing), or temporal segregation (offsetting activity patterns) (Sergio et al. 2007). As Northern Spotted and Barred Owls share similar activity patterns, risk avoidance would likely need to occur through spatial separation, occupation of different habitats, or behavioral shifts that would reduce the frequency of interactions with Barred Owls. All of these solutions can confer direct fitness costs to the individual performing the avoidance behavior through either reduced reproductive capacity or reduced survival (Polis et al. 1989, Lima and Dill 1990, Sunde and Bølstad 2004). Differences in aggressive calling frequency of male Barred and Northern Spotted Owls resulting in Barred Owls' assuming the dominant role during interspecific interactions could explain the apparent reduction in Northern Spotted Owl survival in some areas of co-occurrence (Anthony et al. 2006).

Effects of Covariates

Duration of Territory Occupancy (MY and FY)

The frequency of aggressive calling was not strongly influenced by the male and female years on territory covariates in my analyses incorporating duration of occupancy by Northern Spotted Owls. Although increasing levels of territorial defense have been documented with increasing of years of territory occupation in Song Sparrows (Hyman et. al. 2004), the lack of an effect in this study suggests that if benefits are obtained from an increased amount of time spent on a territory (i.e., knowledge of terrain, established territorial borders, and knowledge of prey location), a single season may be sufficient for residents to realize these benefits.

Female Presence (FP)

The response of a female during a trial was positively correlated with increased male response rates and aggressive calling frequency. Although females in this study, and in past research (Forsman et al. 1984, and Reid et al. 1999), responded less frequently than did males, it appears that their involvement in territorial disputes either escalates the frequency and magnitude of male responses or occurs when defense of the territory is particularly important to the pair.

Seasonality (AD)

The variable accounting for timing within the season (*AD*) was frequently included in the top models of many of my model sets. Of the response variables examined, aggressive calling frequency appeared to be most influenced by *AD*, which is consistent with another playback experiment designed to elicit territorial responses in Northern Spotted Owls (Waldo 2002). Fluctuations in territorial behavior throughout the season are not surprising for several reasons. First, as the season progresses, juvenile Northern Spotted Owls leave the nest and become more vocal, particularly in response to vocalizations by their parents. By reducing the total number of vocalizations on a territory later in the season when juveniles are more likely to respond to parents' vocalizations, it is possible that the resident parents are reducing the risk of drawing predators closer to their young. Additionally, testosterone levels, which affect calling rates in many species of birds (e.g., Balthazart 1983, Hunt et al. 1997), typically decline when parents begin to feed young (Wingfield et al. 1990, Wingfield and Farner 1993). A similar decline in testosterone levels throughout the summer for these two species may explain reduced calling frequencies observed in this study.

Year Effect (YC)

The year when trials were conducted (*YC*) appeared to significantly affect female responsiveness (response code) and response latency; however, it did not appear to influence male territorial responsiveness. Factors such as precipitation and prevalence of wildfires on the study areas differed between the 2008 and 2009 field seasons (personal observation). Both phenomena could potentially alter the magnitude and frequency of territorial responses. Additionally, the potential of a carry-over effect, in which the residents became habituated to the treatment, from year one of the study to year two, may have resulted in lower responsiveness, lower call frequencies, and increased call latency between years one and two in the study.

General Conclusions

My findings suggest that interspecific interactions between Barred and Northern Spotted Owls occur less frequently than intraspecific interactions within Northern Spotted Owls. However, when interactions did occur, male Barred Owls appeared to respond with higher levels of vocal aggression, suggesting that Northern Spotted Owls may act as subordinates during interspecific altercations with Barred Owls. Although the “exclusion” and “acquiescence” hypotheses received mixed support in this study, the apparent dominance by Barred Owls over Northern Spotted Owls during their interactions indicates that competitive exclusion is a plausible mechanism for displacement of Northern Spotted Owls in areas of co-occurrence.

Exclusion of native species by invasive species has frequently occurred in other systems when the invasive species is superior at resource exploitation and exerts dominance in interspecific interference competition (Amarasekare 2002). In my study interspecific interactions were regularly witnessed and results indicated that Barred Owls are likely to assume the dominant role during agonistic encounters. As an invading species, Barred Owls are generalist predators (Hamer et al. 2007) potentially granting them an advantage at resource exploitation. Future studies illuminating whether Barred Owls are truly superior at resource exploitation compared to Northern Spotted Owls would supplement the findings of this research and assist managers in determining if the relationship between these two species matches that explained by Amarasekare (2002), in which competitive exclusion of Northern Spotted Owls by Barred Owls would be the most likely outcome in areas of co-occurrence.

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Table 1.1. Targeted number of replicate trials (*n*) to be conducted by treatment, year, and seasonal period for Barred (BAOW) and Northern Spotted Owl (SPOW) playback experiments in northwestern California. The actual number of replicates conducted are shown in parentheses.

		Treatment†			
Year	**Seasonal Period**	**SPOW / SPOW**	**SPOW / BAOW**	**BAOW / SPOW**	***n***
2008	5/20 – 6/20	7 (7)	7(7)	7 (7)	21 (21)
	6/21 – 7/20	7 (6)	7 (6)	7 (7)	21 (19)
	7/21 – 8/20	7 (8)	7 (11)	7 (5)	21 (24)
2009	5/20 – 6/20	7 (7)	7 (7)	7 (7)	21 (21)
	6/21 – 7/20	7 (7)	7 (7)	7 (6)	21 (20)
	7/21 – 8/20	7 (7)	7 (7)	7 (8)	21 (22)
Total		42 (42)	42 (42)	42 (42)	126 (127)

† For each treatment type the first acronym represents the resident species followed by the playback species that was presented to the resident species.

Table 1.2. Composition of Northern Spotted and Barred Owl vocalizations with respect to call type, number of calls, and silent periods between calls used in playback experimental trials in northwestern California.

Section	**Call Type**	**Sequence Length (sec)**	**Interval Between Sequences (sec)**	**Number of Calls**	**Total Length (min:sec)**	**Start Time (min:sec)**
Spotted Owl:						
1	4-Note	5	15	30	9:45	0:00
2	*Silence*	---	---	0	4:00	9:45
3	4-Note	5	15	30	9:45	13:45
4	*Silence*	---	---	0	4:00	23:30
5	Mixed 1[a]	53	15	30	11:20	27:30
6	*Silence*	---	---	0	4:00	38:50
7	Mixed 2[b]	20	15	20	5:35	42:50
8	*Silence*	---	---	0	4:00	48:25
9	Mixed 3[c]	35	15	24	6:25	52:25
10	*Silence*	---	---	0	1:10	58:50
					END	60:00
Barred Owl:						
1	9-Note	4	15	30	9:15	0:00
2	*Silence*	---	---	0	4:10	9:15
3	9-Note	4	15	30	9:15	13:25
4	*Silence*	---	---	0	4:10	22:45
5	Mixed 1[d]	53	15	30	8:05	26:55
6	*Silence*	---	---	0	4:10	35:00
7	Mixed 2[e]	20	15	20	5:55	39:10
8	*Silence*	---	---	0	4:10	45:45
9	Mixed 3[f]	35	15	24	6:25	49:55
10	*Silence*	---	---	0	3:40	56:20
					END	60:00

[a] Mix 1 = {4-Note (5 sec) + 8 sec + 4-Note (5 sec) + 8 sec + Agitation (7 sec)} Repeated 10 times.

[b] Mix 2 = {Agitation (7 sec) + 8 sec + 4-Note (5 sec)} Repeated 10 times.

[c] Mix 3 = {Agitation (7 sec) + 8 sec + Agitation (7 sec) + 8 sec + 4-Note (5 sec)} Repeated 10 times.

[d] Mix 1 = {9-Note (4 sec) + 8 sec + 9-Note (4 sec) + 8 sec + Agitation (10 sec)} Repeated 10 times.

[e] Mix 2 = {Agitation (7 sec) + 8 sec + 4-Note (5 sec)} Repeated 10 times.

[f] Mix 3 = {Agitation (7 sec) + 8 sec + Agitation (7 sec) + 8 sec + 4-Note (5 sec)} Repeated 10 times.

Table 1.3. Classification of Barred and Northern Spotted Owl vocalizations used in categorizing vocal behavioral responses in playback experiments conducted in northwestern California.

Vocalization Classification	Northern Spotted Owl Call Type†	Barred Owl Call Type††
Territorial	Four Note Call	Nine Note Call - “Who Cooks For You” Six to Nine Note “hoo – aw” Two Note “hoo – aw”
Aggressive	Agitated Location Call	One Syllable Wail or Screech
	Bark Series	Nine Note Duet
	Agitated Contact Call	
	Wraaak! Call	
	Alarm Call	
Contact	Contact Call	Contact Call
	Series Location Call	
Not Applicable	Nest Call	Juvenile Begging Call
	Chitter	
	Female Copulatory Call	
	Male Copulatory Call	
	Cooing Call	
	Juvenile Begging Call	

† Northern Spotted Owl call types described in Forsman 1984.

††Barred Owl call types described in Brewster and Chapman 1891, Bent 1938, McGarigal and Fraser 1985.

Table 1.4. Description of response variables used in analyses of data from experimental playback trials conducted on Barred and Northern Spotted Owl territories in northwestern California.

Response Variable	**Variable Type**	**Description**
Male Response	Categorical	Whether a male responded (1) or did not respond (0) during a trial
Male Aggressive Call Frequency	Continuous	# of male aggressive calls per minute
Male Call Latency	Continuous	# of minutes from start of trial to first male vocal response
Female Response	Categorical	Whether a female responded (1) or did not respond (0) during a trial
Female Aggressive Call Frequency	Continuous	# of female aggressive calls per minute
Female Call Latency	Continuous	# of minutes from start of trial to first female vocal response
Male and Female Response Code	Categorical	Whether a male or female or both sexes responded (1) or did not respond (0) during a trial
Male and Female Aggressive Call Frequency	Continuous	Total # of male and female aggressive calls per minute
Male and Female Call Latency	Continuous	# of minutes from start of trial to first vocal response by either the male or female

Table 1.5. Description of covariates used in analyses of data from experimental playback trials on Barred and Northern Spotted Owls conducted in northwestern California.

Covariate	Covariate Acronym	Variable Type	Description
Treatment Type	TT	Categorical	Combination of resident and playback species for each trial
Study Area	SC	Categorical	Differentiates between interior and coastal study areas.
Adjusted Julian Date	AD	Continuous	# of days after May 20 (the first day of the field season).
Moon Phase	MP	Continuous	# of visible quarters of the moon at the end of the trial.
Truncation Code	TC	Categorical	Delineates whether or not the trial was truncated for any reason.
Year Code	YC	Categorical	Differentiates between the 2008 and 2009 field seasons.
UTM Days	UD	Continuous	# of days between the last known owl location and the playback trial.
Reproductive Code	RC	Categorical	Residents are known to be reproductively active, inactive, or of undetermined status.
Pair Code	PC	Categorical	Residents are known to be single, paired, or of undetermined pair status.
Female Presence	FP	Categorical	Describes whether or not the resident female was seen or heard during the trial.
Male Territory Years	MY	Continuous	# of years the individual male resident has been found on the current territory.
Female Territory Years	FY	Continuous	# of years the individual female resident has been found on the current territory.

Table 1.6. Ranking of *a priori* and *a posteriori* models used to analyze male Barred and Northern Spotted Owl responses to 126 experimental playback trials conducted in northwestern California. AICc is a small sample size correction factor for AIC. ΔAICc is the difference in AICc units between a given model and the top-ranking model. Akaike weight is the probability that a given model is the best-approximating model of the models tested. Covariates included in the models are described in Table 1.5.

Model	***R^2***	**K**	**AIC**	**AICc**	**ΔAICc**	**Akaike Weight**
TT + FP	0.28	4	146.15	146.48	0.00	0.85
TT + FP + TT*FP	0.28	6	149.31	150.01	3.53	0.15
TT	0.08	3	164.51	164.71	18.23	0.00
TT + AD	0.09	4	165.64	165.97	19.50	0.00
TT + SC	0.09	4	166.19	166.52	20.04	0.00
TT + TC	0.09	4	166.24	166.57	20.09	0.00
TT + YC	0.08	4	166.43	166.76	20.28	0.00
TT + EM	0.08	4	166.46	166.79	20.31	0.00
TT + UD	0.08	4	166.51	166.84	20.36	0.00
TT + RC + RC*TT	0.17	8	166.12	167.35	20.87	0.00
TT + RC	0.10	5	167.30	167.80	21.32	0.00
TT + PC	0.09	5	167.75	168.25	21.77	0.00
Intercept Only	0.00	1	168.46	168.49	22.01	0.00
TT + RC + AD + RC*TT†	0.17	10	169.51	169.78	23.30	0.00
TT + RC + AD + RC*AD	0.14	9	170.49	172.04	25.56	0.00
TT + RC + AD + RC*TT + RC*TT*AD	0.20	13	172.51	175.76	29.28	0.00

† *a posteriori* model

Table 1.7. Model-averaged estimates and 95% confidence intervals for treatment effects of Barred Owl residents presented with Northern Spotted Owl treatment (BAOW/SPOW) and Spotted Owl residents presented with Barred Owl treatment (SPOW/BAOW) relative to trials in which Northern Spotted Owl residents were presented with the Northern Spotted Owl treatment (SPOW/SPOW) (*n* = 126 trials).

	BAOW/SPOW Treatment†		**SPOW/BAOW Treatment†**	
Model Set	**Estimate**	**95% CI**	**Estimate**	**95% CI**
All Trials				
Male Response Code	−0.47	−1.09, 0.16	−0.11	−0.69, 0.48
Female Response Code	−0.69	−1.35, −0.02	0.37	−0.21, 0.95
Male and Female Response Code	−0.75	−1.31, −0.20	0.11	−0.45, 0.66
Male Calling Frequency	0.83	−0.09, 1.75	−0.46	−1.00, 0.07
Female Calling Frequency	0.05	−0.18, 0.29	0.20	−0.01, 0.42
Male and Female Calling Frequency	0.00	−0.69, 0.69	−0.26	−1.07, 0.54
Male Vocal Response Latency	7.00	−9.71, 23.71	−1.14	−13.43, 10.60
Female Vocal Response Latency	15.78	5.58, 25.98	0.88	−8.99, 10.76
Male and Female Vocal Response Latency	22.42	11.94, 32.89	2.57	−8.05, 13.18

†For each treatment type the first 4-letter AOU code listed represents the resident species followed by the playback species that was presented.

Table 1.8. Ranking of *a priori* and *a posteriori* models used to analyze female Barred and Northern Spotted Owl responses to 126 experimental playback trials conducted in northwestern California. AICc is a small sample size correction factor for AIC. ΔAICc is the difference in AICc units between a given model and the top-ranking model. Akaike weight is the probability that a given model is the best-approximating model of the models tested within the model set. Covariates included in the models are described in Table 1.5.

Model	R^2	**K**	**AIC**	**AICc**	**ΔAICc**	**Akaike Weight**
TT + YC	0.13	4	163.46	163.79	0.00	0.54
TT + RC + YC + RC*TT[†]	0.23	10	164.53	166.44	2.66	0.14
TT + RC + RC*TT	0.18	8	166.59	167.82	4.03	0.07
TT	0.07	3	168.16	168.36	4.57	0.06
TT + AD	0.08	4	168.79	169.12	5.33	0.04
TT + SC	0.07	4	169.43	169.76	5.97	0.03
TT + EM	0.07	4	169.89	170.22	6.43	0.02
TT + UD	0.07	4	170.06	170.39	6.61	0.02
Intercept Only	0.00	1	170.40	170.43	6.65	0.02
TT + TC	0.07	4	170.16	170.49	6.71	0.02
TT + RC	0.08	5	170.25	170.75	6.97	0.02
TT, RC, AD, RC*AD	0.15	8	169.82	171.05	7.26	0.01
TT + RC + AD + RC*TT + RC*TT*AD	0.26	14	169.05	172.83	9.04	0.01

[†] *a posteriori* model

Table 1.9. Ranking of *a priori* models used to analyze Barred and Northern Spotted Owl responses by territory (male and/or female responding) to 126 experimental playback trials conducted in northwestern California. AICc is a small sample size correction factor for AIC. ΔAICc is the difference in AICc units between a given model and the top-ranking model. Akaike weight is the probability that a given model is the best-approximating model of the models tested within the model set. Covariates included in the models are described in Table 1.5.

Model	R^2	**K**	**AIC**	**AICc**	**ΔAICc**	**Akaike Weight**
TT	0.09	3	155.04	155.24	0.00	0.25
TT + AD	0.10	4	156.17	156.50	1.26	0.13
TT + YC	0.09	4	156.78	157.11	1.87	0.10
TT + UD	0.09	4	156.78	157.11	1.87	0.10
TT + EM	0.09	4	156.93	157.26	2.02	0.09
TT + TC	0.09	4	157.00	157.33	2.09	0.09
TT + SC	0.09	4	157.01	157.34	2.10	0.09
TT + PC	0.10	5	157.80	158.30	3.06	0.05
TT + RC	0.10	5	158.03	158.53	3.29	0.05
TT + RC + AD + RC*AD	0.16	8	158.26	159.49	4.25	0.03
Intercept Only	0.00	1	159.49	159.52	4.28	0.03

Table 1.10. Ranking of *a priori* and *a posteriori* models used to analyze male Barred and Northern Spotted Owl aggressive call frequency to 126 experimental playback trials conducted in northwestern California. AICc is a small sample size correction factor for AIC. ΔAICc is the difference in AICc units between a given model and the top-ranking model. Akaike weight is the probability that a given model is the best-approximating model of the models tested within the model set. Covariates included in the models are described in Table 1.5.

Model	R^2	**K**	**AIC**	**AICc**	**ΔAICc**	**Akaike Weight**
TT + FP + SC + AD + TT*FP[†]	0.30	9	339.79	341.34	0.00	0.55
TT + FP + SC + AD + FP*AD[†]	0.27	8	342.77	344.00	2.66	0.15
TT + FP + AD + FP*AD	0.26	7	343.28	344.23	2.89	0.13
TT + FP + TT*FP	0.26	7	343.53	344.48	3.14	0.12
TT + FP + SC + TT*FP[†]	0.26	8	344.68	345.91	4.57	0.06
TT + FP	0.18	5	351.06	351.56	10.21	0.00
TT + RC + FP + RC*FP	0.23	9	351.72	353.28	11.93	0.00
TT + AD + TT*AD	0.11	7	366.50	367.45	26.10	0.00
TT + AD	0.07	5	367.06	367.56	26.22	0.00
Intercept Only	0.00	2	370.71	370.81	29.46	0.00
TT	0.03	4	371.46	371.79	30.45	0.00
TT + SC	0.04	5	371.44	371.94	30.59	0.00
TT + YC	0.03	5	372.98	373.48	32.13	0.00
TT + UD	0.03	5	373.32	373.82	32.47	0.00
TT + TC	0.03	5	373.35	373.85	32.51	0.00
TT + EM	0.03	5	373.50	373.95	32.61	0.00
TT + RC + RC*TT	0.10	10	373.02	374.94	33.59	0.00
TT + RC + AD + RC*AD	0.08	9	373.79	375.34	34.00	0.00
TT + PC	0.03	6	374.79	375.49	34.15	0.00
TT + RC	0.03	6	375.38	376.09	34.74	0.00

[†] *a posteriori* model.

Table 1.11. Ranking of *a priori* and *a posteriori* models used to analyze female Barred and Northern Spotted Owl aggressive calling frequency to 126 experimental playback trials conducted in northwestern California. AICc is a small sample size correction factor for AIC. ΔAICc is the difference in AICc units between a given model and the top-ranking model. Akaike weight is the probability that a given model is the best-approximating model of the models tested within the model set. Covariates included in the models are described in Table 1.5.

Model	R^2	**K**	**AIC**	**AICc**	**ΔAICc**	**Akaike Weight**
TT + YC + RC[†]	0.09	7	188.64	189.59	0.00	0.20
TT + YC	0.06	5	189.66	190.16	0.56	0.15
TT + RC	0.07	6	189.67	190.38	0.78	0.13
TT	0.04	4	190.12	190.45	0.86	0.13
Intercept Only	0.00	2	190.79	190.89	1.30	0.10
TT + SC	0.04	5	191.73	192.23	2.64	0.05
TT + AD	0.04	5	191.77	192.27	2.68	0.05
TT + UD	0.04	5	191.91	192.41	2.82	0.05
TT + EM	0.04	5	192.00	192.50	2.91	0.05
TT + TC	0.04	5	192.08	192.58	2.99	0.04
TT + PC	0.04	6	193.70	194.40	4.81	0.02
TT + RC + AD + RC*AD	0.09	9	193.56	195.11	5.52	0.01
TT + AD + TT*AD	0.04	7	195.70	196.64	7.05	0.01
TT + RC + RC*TT	0.09	10	194.76	196.67	7.08	0.01

[†] *a posteriori* model

Table 1.12. Ranking of *a priori* models used to analyze Barred and Northern Spotted Owl aggressive call frequency at the level of the territory (male and/or female responding) to 126 experimental playback trials conducted in northwestern California. AICc is a small sample size correction factor for AIC. ΔAICc is the difference in AICc units between a given model and the top-ranking model. Akaike weight is the probability that a given model is the best-approximating model of the models tested within the model set. Covariates included in the models are described in Table 1.5.

Model	R^2	**K**	**AIC**	**AICc**	**ΔAICc**	**Akaike Weight**
Intercept Only	0.00	2	412.53	412.62	0.00	0.49
TT + AD	0.03	5	414.61	415.11	2.49	0.14
TT + AD + TT*AD	0.06	7	415.20	416.15	3.53	0.08
TT	0.00	4	416.09	416.42	3.79	0.07
TT + SC	0.02	5	415.99	416.49	3.87	0.07
TT + UD	0.01	5	417.83	418.33	5.71	0.03
TT + TC	0.00	5	418.05	418.55	5.92	0.03
TT + YC	0.00	5	418.08	418.58	5.96	0.03
TT + EM	0.00	5	418.08	418.58	5.96	0.03
TT + RC + RC*TT	0.09	10	417.30	419.21	6.58	0.02
TT + PC	0.01	6	419.23	419.93	7.31	0.01
TT + RC	0.01	6	419.70	420.40	7.78	0.01
TT + RC + AD + RC*AD	0.05	9	420.61	422.17	9.54	0.00

Table 1.13. Ranking of *a priori* and *a posteriori* models used to analyze male Barred and Northern Spotted Owl aggressive call frequency, conditional upon a response, to 79 experimental playback trials conducted in northwestern California. AICc is a small sample size correction factor for AIC. ΔAICc is the difference in AICc units between a given model and the top-ranking model. Akaike weight is the probability that a given model is the best-approximating model of the models tested within the model set. Covariates included in the models are described in Table 1.5.

Model	R^2	**K**	**AIC**	**AICc**	**ΔAICc**	**Akaike Weight**
TT+ FP + AD + TT*AD[†]	0.38	8	221.93	223.96	0.00	0.73
TT + AD + TT*AD	0.33	7	225.98	227.54	3.58	0.12
TT + FP + AD + FP*AD	0.32	7	227.59	229.15	5.19	0.05
TT + RC + FP + AD + RC*AD[†]	0.38	10	226.36	229.54	5.59	0.05
TT + AD	0.27	5	229.45	230.26	6.31	0.03
TT + RC + AD + RC*AD	0.34	9	229.11	231.68	7.72	0.02
TT + FP + AD + FP*AD	0.20	5	236.15	236.96	13.00	0.00
TT + FP + TT*FP	0.24	7	236.07	237.62	13.66	0.00
TT + RC + FP + RC*FP	0.28	9	236.60	239.17	15.21	0.00
TT + RC + RC*TT	0.28	10	237.69	240.88	16.93	0.00
TT	0.13	4	241.44	241.97	18.01	0.00
TT + SC	0.15	5	241.36	242.17	18.21	0.00
TT +UD	0.13	5	242.71	243.52	19.56	0.00
TT + YC	0.13	5	242.88	243.69	19.74	0.00
TT + TC	0.13	5	243.09	243.90	19.95	0.00
TT + EM	0.13	5	243.39	244.20	20.2	0.00
TT + PC	0.14	6	244.44	245.59	21.63	0.00
TT + RC	0.13	6	245.40	246.55	22.59	0.00
Intercept Only	0.00	2	247.98	248.14	24.18	0.00

[†] *a posteriori* model

Table 1.14. Model-averaged estimates and 95% confidence intervals for treatment effects of Barred Owl residents presented with Northern Spotted Owl treatment (BAOW/SPOW) and Spotted Owl residents presented with Barred Owl treatment (SPOW/BAOW) relative to trials in which Northern Spotted Owl residents were presented with the Northern Spotted Owl treatment (SPOW/SPOW).

	BAOW/SPOW Treatment†		**SPOW/BAOW Treatment†**	
Model Set	**Estimate**	**95% CI**	**Estimate**	**95% CI**
For trials where number of years spent on territory was available				
Male Calling Frequency	—§	—§	−0.55	−1.29, 0.28
Female Calling Frequency	—§	—§	0.14	−0.08, 0.35
For trials where a male responded				
Male Calling Frequency	1.04	0.01, 2.08	−1.22	−2.33, −0.11
Male Vocal Response Latency	7.71	−7.16, 22.57	−5.40	−10.85, 0.05
For trials where a female responded				
Female Calling Frequency	0.29	−0.27, 0.84	0.41	−0.03, 0.86
Female Vocal Response Latency	14.93	−21.22, 51.08	4.99	−5.71, 15.69
For trials where a male or female responded				
Male and Female Calling Frequency	0.97	-0.30, 2.25	−0.50	−1.86, 0.87
Male and Female Vocal Response Latency	13.67	7.45, 19.90	−2.74	−9.46, 3.99

† For each treatment type the first 4-letter AOU code listed represents the resident species followed by the playback species that was presented.

§Data not available for the analysis

Table 1.15. Ranking of *a priori* and *a posteriori* models used to analyze female Barred and Northern Spotted Owl aggressive call frequency, conditional upon a response, to 49 experimental playback trials conducted in northwestern California. AICc is a small sample size correction factor for AIC. ΔAICc is the difference in AICc units between a given model and the top-ranking model. Akaike weight is the probability that a given model is the best-approximating model of the models tested within the model set. Covariates included in the models are described in Table 1.5.

Model	R^2	**K**	**AIC**	**AICc**	**ΔAICc**	**Akaike Weight**
TT + RC	0.19	6	110.88	112.88	0.00	0.25
Intercept Only	0.00	2	113.01	113.27	0.39	0.21
TT	0.08	4	113.09	114.00	1.12	0.14
TT + AD	0.10	5	113.67	115.07	2.19	0.08
TT + RC + AD[†]	0.19	7	112.62	115.35	2.47	0.07
TT + YC	0.08	5	114.87	116.26	3.38	0.05
TT + UD	0.08	5	114.93	116.33	3.44	0.05
TT + SC	0.08	5	114.97	116.36	3.48	0.04
TT + TC	0.08	5	115.07	116.46	3.58	0.04
TT + EM	0.08	5	115.09	116.48	3.60	0.04
TT + PC	0.08	6	117.05	119.05	6.17	0.01
TT + AD + TT*AD	0.11	7	117.33	120.07	7.18	0.01
TT + RC + AD + RC*AD	0.19	9	116.48	121.10	8.22	0.00
TT + RC + RC*TT	0.20	10	118.13	123.92	11.04	0.00

[†] *a posteriori* model

Table 1.16. Ranking of *a priori* models used to analyze Barred and Northern Spotted Owl aggressive call frequency at the level of the territory for trials in which a response was detected for 86 playback experimental trials conducted in northwestern California. AICc is a small sample size correction factor for AIC. ΔAICc is the difference in AICc units between a given model and the top-ranking model. Akaike weight is the probability that a given model is the best-approximating model of the models tested within the model set. Covariates included in the models are described in Table 1.5.

Model	**R^2**	**K**	**AIC**	**AICc**	**ΔAICc**	**Akaike Weight**
TT + AD + TT*AD	0.20	7	285.25	286.69	0.00	0.48
TT + AD	0.14	5	286.89	287.64	0.96	0.30
TT + RC + AD + RC*AD	0.22	9	287.19	289.56	2.87	0.11
TT + RC + RC*TT	0.22	10	288.92	291.86	5.17	0.04
TT	0.06	4	292.93	293.43	6.74	0.02
TT + SC	0.08	5	292.82	293.57	6.89	0.02
Intercept Only	0.00	2	294.03	294.18	7.49	0.01
TT + UD	0.07	5	293.85	294.60	7.92	0.01
TT + EM	0.06	5	294.86	295.61	8.92	0.01
TT + YC	0.06	5	294.93	295.68	8.99	0.01
TT + TC	0.06	5	294.93	295.68	9.00	0.01
TT + PC	0.07	6	295.94	297.01	10.32	0.00
TT + RC	0.07	6	296.01	297.07	10.39	0.00

Table 1.17. Ranking of *a priori* and *a posteriori* models used to analyze the effect of duration of territory occupancy on male Northern Spotted Owl aggressive call frequency for 84 playback experimental trials conducted in northwestern California. AICc is a small sample size correction factor for AIC. ΔAICc is the difference in AICc units between a given model and the top-ranking model. AICc weight is the probability that a given model is the best-approximating model of the models tested within the model set. Covariates included in the models are described in Table 1.5.

Model	***R^2***	**K**	**AIC**	**AICc**	**ΔAICc**	**Akaike Weight**
TT + FP + AD + FP*AD	0.22	6	211.22	212.31	0.00	0.27
TT + FP + AD + TT*AD[†]	0.24	7	210.98	212.45	0.14	0.25
TT + FP + AD + MY + FP*AD[†]	0.24	7	211.02	212.50	0.19	0.25
TT + FP + AD[†]	0.17	5	214.36	215.13	2.82	0.07
TT + RC + MY + AD + FP + RC*MY + RC*MY*AD[†]	0.35	13	210.28	215.48	3.17	0.06
TT + AD + TT*AD	0.16	5	215.26	216.03	3.71	0.04
TT + FP	0.13	4	216.50	217.00	4.69	0.03
TT + FP + TT*FP	0.15	5	216.71	217.48	5.17	0.02
TT + RC + MY + AD + RC*MY + RC*MY*AD	0.30	12	215.58	219.98	7.67	0.01
TT + RC + FP + RC +FP	0.19	8	218.81	220.73	8.42	0.00
TT + AD	0.09	4	220.48	220.98	8.67	0.00
TT + FP + AD + MY + TT*AD[†]	0.18	8	219.37	221.29	8.98	0.00
TT + RC + AD + RC*AD	0.17	8	220.77	222.69	10.38	0.00
TT + MY	0.06	4	222.99	223.49	11.18	0.00
TT + RC	0.09	5	222.73	223.50	11.19	0.00
TT + RC + RC*TT	0.13	7	222.55	224.02	11.71	0.00
TT	0.03	3	223.84	224.14	11.83	0.00

Table continued…

Table continued…

Intercept Only	0.00	2	224.32	224.47	12.16	0.00
TT + YC	0.05	4	224.30	224.81	12.50	0.00
TT + TC	0.05	4	224.46	224.96	12.65	0.00
TT + RC + MY + RC*MY	0.15	8	223.30	225.22	12.91	0.00
TT + SC	0.04	4	225.23	225.74	13.43	0.00
TT + EM	0.03	4	225.72	226.23	13.92	0.00
TT + UD	0.03	4	225.84	226.35	14.04	0.00
TT + PC	0.04	5	226.93	227.69	15.38	0.00

† *a posteriori* model

Table 1.18. Ranking of *a priori* models used to analyze the effect of duration of territory occupancy on female Northern Spotted Owl aggressive call frequency for 80 experimental playback trials conducted in northwestern California. AICc is a small sample size correction factor for AIC. ΔAICc is the difference in AICc units between a given model and the top-ranking model. AICc weight is the probability that a given model is the best-approximating model of the models tested within the model set. Covariates included in the models are described in Table 1.5.

Model	***R^2***	**K**	**AIC**	**AICc**	**ΔAICc**	**Akaike Weight**
Intercept Only	0.00	2	111.99	112.14	0.00	0.20
TT	0.02	3	112.36	112.67	0.53	0.16
TT + EM	0.05	4	112.31	112.85	0.70	0.14
TT + UD	0.04	4	112.65	113.19	1.04	0.12
TT + FY	0.04	4	113.25	113.78	1.64	0.09
TT + AD	0.02	4	114.20	114.73	2.59	0.06
TT + YC	0.02	4	114.22	114.76	2.61	0.06
TT + SC	0.02	4	114.28	114.81	2.67	0.05
TT + TC	0.02	4	114.33	114.86	2.72	0.05
TT + RC	0.04	5	115.05	115.86	3.72	0.03
TT + PC	0.02	5	116.10	116.91	4.77	0.02
TT + AD + TT*AD	0.02	5	116.20	117.01	4.87	0.02
TT + RC + RC*TT	0.04	7	118.55	120.10	7.96	0.00
TT + RC + FY + RC*FY	0.06	8	119.42	121.45	9.31	0.00
TT + RC + AD + RC*AD	0.05	8	120.16	122.19	10.05	0.00
TT + RC + FY + AD + RC*FY + RC*FY*AD	0.07	12	126.83	131.48	19.34	0.00

Table 1.19. Ranking of *a priori* and *a posteriori* models used to analyze male Barred and Northern Spotted Owl vocal response latency to 126 playback experimental trials conducted in northwestern California. AICc is a small sample size correction factor for AIC. ΔAICc is the difference in AICc units between a given model and the top-ranking model. Akaike weight is the probability that a given model is the best-approximating model of the models tested within the model set. Covariates included in the models are described in Table 1.5.

Model	R^2	**K**	**AIC**	**AICc**	**ΔAICc**	**Akaike Weight**
TT + TC + FP + AD + FP*AD	0.29	8	1139.93	1141.16	0.00	0.23
TT + TC + FP + AD + TT*FP†	0.30	9	1139.86	1141.41	0.25	0.20
TT + TC + FP + AD†	0.28	7	1140.53	1141.48	0.32	0.19
TT + TC + FP + TT*FP	0.29	8	1140.72	1141.95	0.78	0.15
TT + TC + FP	0.26	6	1141.64	1142.35	1.19	0.13
TT + TC + FP + RC + AD + TT*FP†	0.31	11	1141.69	1144.01	2.85	0.05
TT + TC + FP + RC + AD + FP*AD†	0.29	10	1143.44	1145.35	4.19	0.03
TT + TC + FP + RC†	0.26	8	1144.77	1146.00	4.84	0.02
TT + TC + RC + FP + RC*FP	0.26	10	1148.45	1150.36	9.20	0.00
TT + TC	0.14	5	1158.67	1159.17	18.01	0.00
TT + TC + AD	0.15	6	1159.28	1159.98	18.82	0.00
TT + TC + SC	0.14	6	1160.45	1161.15	19.99	0.00
TT + TC + YC	0.14	6	1160.61	1161.31	20.15	0.00
TT + TC + EM	0.14	6	1160.66	1161.37	20.20	0.00
TT + TC + UD	0.14	6	1160.67	1161.37	20.21	0.00
TT + TC + RC	0.15	7	1160.91	1161.86	20.69	0.00
TT + TC + RC + AD + RC*AD	0.19	10	1159.96	1161.87	20.71	0.00
TT + TC + PC	0.14	7	1162.23	1163.18	22.01	0.00

Table continued…

Table continued…

TT + TC + AD + TT*AD	0.15	8	1162.96	1164.19	23.02	0.00
TT + TC + RC + RC*TT	0.19	11	1162.26	1164.57	23.41	0.00
Intercept Only	0.00	2	1171.01	1171.11	29.95	0.00

† *a posteriori* model.

Table 1.20. Ranking of *a priori* and *a posteriori* models used to analyze female Barred and Northern Spotted Owl vocal response latency to 126 playback experimental trials conducted in northwestern California. AICc is a small sample size correction factor for AIC. ΔAICc is the difference in AICc units between a given model and the top-ranking model. Akaike weight is the probability that a given model is the best-approximating model of the models tested within the model set. Covariates included in the models are described in Table 1.5.

Model	R^2	**K**	**AIC**	**AICc**	**ΔAICc**	**Akaike Weight**
TT + TC + YC	0.17	6	1155.57	1156.28	0.00	0.34
TT + TC + YC + AD†	0.18	7	1156.14	1157.09	0.81	0.23
TT + TC	0.14	5	1158.00	1158.50	2.22	0.11
TT + TC + AD	0.15	6	1158.51	1159.22	2.94	0.08
TT + TC + PC	0.16	7	1158.87	1159.82	3.54	0.06
TT + TC + SC	0.15	6	1159.28	1159.99	3.71	0.05
TT + TC + EM	0.15	6	1159.51	1160.21	3.94	0.05
TT + TC + UD	0.14	6	1159.86	1160.57	4.29	0.04
TT + TC + RC	0.15	7	1160.99	1161.94	5.66	0.02
TT + TC + RC + AD + RC*AD	0.19	10	1160.89	1162.80	6.52	0.01
TT + TC + AD + TT*AD	0.15	8	1162.14	1163.37	7.09	0.01
TT + TC + RC + RC*TT	0.18	11	1164.52	1166.84	10.56	0.00
Intercept Only	0.00	2	1171.19	1171.29	15.01	0.00

† *a posteriori* model

Table 1.21. Ranking of *a priori* models used to analyze Barred and Northern Spotted Owl vocal response latency at the territory level (male and/or female responding) to 126 experimental playback trials conducted in northwestern California. AICc is a small sample size correction factor for AIC. ΔAICc is the difference in AICc units between a given model and the top-ranking model. Akaike weight is the probability that a given model is the best-approximating model of the models tested within the model set. Covariates included in the models are described in Table 1.5.

Model	***R^2***	**K**	**AIC**	**AICc**	**ΔAICc**	**Akaike Weights**
TT + TC	0.18	5	1152.21	1152.71	0.00	0.24
TT + TC + AD	0.19	6	1152.84	1153.55	0.84	0.16
TT + TC + RC + AD + RC*AD	0.25	10	1151.84	1153.75	1.04	0.14
TT + TC + YC	0.19	6	1153.49	1154.20	1.48	0.11
TT + TC + EM	0.19	6	1154.01	1154.71	2.00	0.09
TT + TC + UD	0.19	6	1154.05	1154.76	2.05	0.09
TT + TC + SC	0.18	6	1154.21	1154.91	2.20	0.08
TT + TC + RC	0.19	7	1155.15	1156.10	3.38	0.04
TT + TC + PC	0.19	7	1155.99	1156.94	4.22	0.03
TT + TC + RC + RC*TT	0.24	11	1155.46	1157.78	5.06	0.02
TT + TC + AD + TT*AD	0.19	8	1156.57	1157.80	5.08	0.02
Intercept Only	0.00	2	1171.77	1171.86	19.15	0.00

Table 1.22. Ranking of *a priori* and *a posteriori* models used to analyze male Barred and Northern Spotted Owl vocal response latency, conditional upon a response, to 79 experimental playback trials conducted in northwestern California. AICc is a small sample size correction factor for AIC. ΔAICc is the difference in AICc units between a given model and the top-ranking model. Akaike weight is the probability that a given model is the best-approximating model of the models tested within the model set. Covariates included in the models are described in Table 1.5.

Model	***R*^{2}**	**K**	**AIC**	**AICc**	**ΔAICc**	**Akaike Weight**
TT + TC	0.21	5	594.24	595.06	0.00	0.20
TT + TC + SC	0.22	6	594.53	595.70	0.64	0.15
TT + TC + YC	0.21	6	595.75	596.91	1.86	0.08
TT + TC + RC	0.23	7	595.44	597.01	1.96	0.08
TT + TC + UD	0.21	6	596.08	597.25	2.19	0.07
TT + TC + EM	0.21	6	596.10	597.26	2.21	0.07
TT + TC + AD	0.21	6	596.14	597.31	2.25	0.07
TT + TC + FP + RC + AD + FP*AD†	0.27	9	594.72	597.33	2.28	0.07
TT + TC + FP	0.21	6	596.23	597.40	2.34	0.06
TT + TC + FP + AD + FP*AD	0.25	8	596.13	598.19	3.13	0.04
TT + TC + PC	0.22	7	596.69	598.27	3.21	0.04
TT + TC + RC + RC*TT	0.31	11	595.00	598.94	3.88	0.03
TT + TC + FP + TT*FP	0.23	8	597.62	599.68	4.62	0.02
TT + TC + AD + TT*AD	0.23	8	598.05	600.10	5.05	0.02
TT + TC + FP + SC + AD + FP*AD†	0.28	10	597.99	601.23	6.17	0.01
TT + TC + RC + FP + RC*FP	0.24	10	601.12	604.35	9.29	0.00
TT + TC + RC + AD + RC*AD	0.23	10	601.42	604.65	9.59	0.00
Intercept Only	0.00	2	606.43	606.59	11.53	0.00

† *a posteriori* model

Table 1.23. Ranking of *a priori* and *a posteriori* models used to analyze female Barred and Northern Spotted Owl vocal response latency, conditional upon a response, to 49 experimental playback trials conducted in northwestern California. AICc is a small sample size correction factor for AIC. ΔAICc is the difference in AICc units between a given model and the top-ranking model. Akaike weight is the probability that a given model is the best-approximating model of the models tested within the model set. Covariates included in the models are described in Table 1.5.

Model	***R^2***	**K**	**AIC**	**AICc**	**ΔAICc**	**Akaike Weight**
TT + TC + UD	0.24	6	407.06	409.06	0.00	0.26
TT + TC	0.18	5	408.52	409.92	0.85	0.17
TT + TC + AD + TT*AD	0.30	8	407.24	410.84	1.78	0.11
TT + TC + AD	0.20	6	409.26	411.26	2.19	0.09
TT + TC + AD + UD†	0.25	7	408.68	411.41	2.34	0.08
TT + TC + AD + UD + TT*AD†	0.32	9	407.53	412.14	3.08	0.06
TT + TC + EM	0.19	6	410.38	412.38	3.32	0.05
TT + TC + YC	0.18	6	410.52	412.52	3.45	0.05
TT + TC + SC	0.18	6	410.52	412.52	3.46	0.05
Intercept Only	0.00	2	412.43	412.69	3.62	0.04
TT + TC + RC	0.20	7	411.81	414.54	5.48	0.02
TT + TC + PC	0.18	7	412.48	415.21	6.14	0.01
TT + TC + RC + RC*TT	0.36	11	408.31	415.45	6.38	0.01
TT + TC + RC + AD + RC*AD	0.22	10	416.39	422.18	13.12	0.00

† *a posteriori* model

Table 1.24. Ranking of *a priori* models used to analyze vocal response latency of Barred and Northern Spotted Owls at the territory level, conditional upon a response, to 86 experimental playback trials conducted in northwestern California. AICc is a small sample size correction factor for AIC. ΔAICc is the difference in AICc units between a given model and the top-ranking model. Akaike weight is the probability that a given model is the best-approximating model of the models tested within the model set. Covariates included in the models are described in Table 1.5.

Model	***R^2***	**K**	**AIC**	**AICc**	**ΔAICc**	**Akaike Weight**
TT + TC	0.31	5	638.43	639.18	0.46	0.25
TT + TC + SC	0.33	6	638.41	639.48	0.75	0.21
TT + TC + PC	0.33	7	639.57	641.00	2.28	0.10
TT + TC + EM	0.31	6	640.17	641.23	2.51	0.09
TT + TC + YC	0.31	6	640.31	641.38	2.65	0.08
TT + TC + AD	0.31	6	640.40	641.46	2.74	0.08
TT + TC + UD	0.31	6	640.43	641.49	2.77	0.08
TT + TC + RC + RC*TT	0.40	11	638.95	642.51	3.79	0.05
TT + TC + RC	0.32	7	641.25	642.68	3.96	0.04
TT + TC + AD + TT*AD	0.33	8	642.57	644.44	5.72	0.02
TT + TC + RC + AD + RC*AD	0.33	10	645.46	648.39	9.67	0.00
Intercept Only	0.00	2	664.35	664.49	25.77	0.00

Table 1.25. Relative support for the “exclusion” and “acquiescence” hypotheses based on model-averaged treatment type (TT) effects on response code, aggressive calling frequency, and vocal response latency for the all inclusive and conditional analyses. (+) indicates weak support for the hypothesis (i.e., 95% CI for (TT) barely overlapped zero), (+ +) indicates strong support for the hypothesis (i.e., the 95% confidence interval for (TT) did not overlap zero), (0) indicates no substantial difference among treatments (i.e., 95% CI strongly overlapped 0), (−) indicates weak evidence against the hypothesis (i.e., 95% CI for (TT) barely overlapped zero), and (− −) indicates strong evidence against the hypothesis (i.e., 95% CI for (TT) did not overlap zero).

	All Trials		**Trials with a response only**	
Response Variable	“Exclusion” Hypothesis BAOW/SPOW† Treatment	“Acquiescence” Hypothesis SPOW/BAOW† Treatment	“Exclusion” Hypothesis BAOW/SPOW† Treatment	“Acquiescence” Hypothesis SPOW/BAOW† Treatment
Response Code				
Male	−	0	—§	—§
Female	− −	−	—§	—§
Territory	− −	0	—§	—§
Aggressive Call Frequency				
Male	+	+	+ +	+ +
Female	0	+	+	+
Territory	0	0	+	0
Vocal Response Latency				
Male	0	0	−	+
Female	− −	0	0	0
Territory	− −	0	+ +	0

† For each treatment type the first acronym represents the resident species followed by the playback species that was presented to the resident species.

§ not applicable

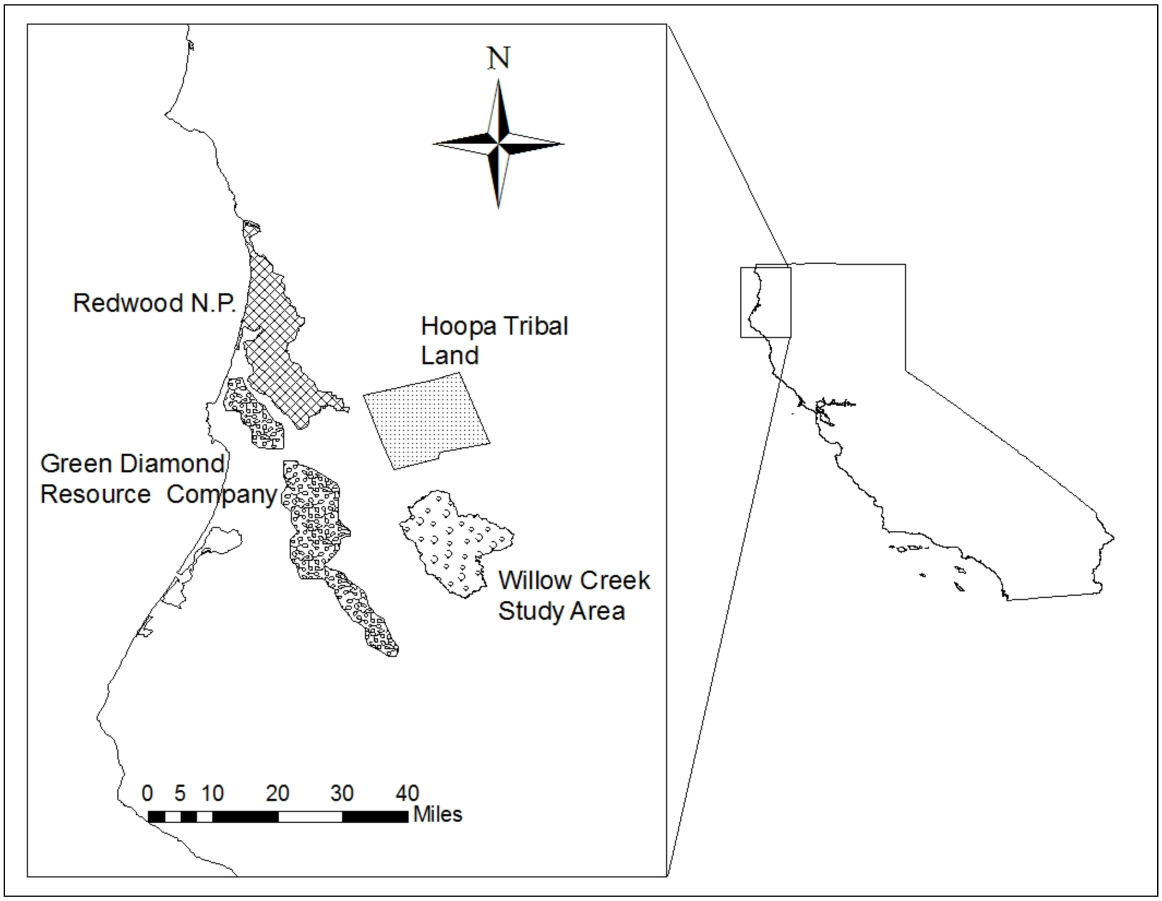

Figure 1.1. Locations of the four study sites located in northwestern California where experimental playback experiments were conducted on Barred and Northern Spotted Owls. Study sites included Green Diamond Resource Company (GDRC), Redwood National Park (RNP), Hoopa Tribal Lands (Hoopa), and Willow Creek Study Area (WCSA).

CHAPTER 2

PHYSICAL DEFENSE OF TERRITORIES BY NORTHERN SPOTTED AND BARRED OWLS

INTRODUCTION

The conservation of the Northern Spotted Owl (*Strix occidentalis caurina*) has been a subject of much concern over the past four decades. Observed population declines likely resulting from habitat loss led to the official listing of the Northern Spotted Owl as a threatened species in 1990 (U.S. Fish and Wildlife Service 1990). The threatened status of the Northern Spotted Owl focused conservation efforts on protecting older forest that was considered suitable Northern Spotted Owl habitat. Northern Spotted Owl populations have continued to decline despite adoption of the Northwest Forest Plan in 1994, which called for stricter regulation of timber harvest throughout the Northern Spotted Owl's range (USDA Forest Service and BLM 1994, Anthony et al. 2006). Competition between Northern Spotted and Barred Owls (*Strix varia*) has been identified as another important potential threat to Northern Spotted Owl populations (Taylor and Forsman 1976, Hamer et al. 1994, Kelly et al. 2003, Anthony et al. 2006, Buchanan et al. 2007, Gutiérrez et al. 2007).

Barred Owls were historically restricted to the eastern portion of the United States. Over the past fifty years their range has expanded to completely overlap that of the Northern Spotted Owl (Dark et al. 1998 and Kelly et al. 2003). Rapidly increasing

Barred Owl populations coupled with continued Northern Spotted Owl population declines lend support to the idea that competition with the Barred Owl may represent a very real threat to remaining Northern Spotted Owl populations. Over the past decade, studies investigating the potential impact of Barred Owls on Northern Spotted Owl populations have shown that occupancy, colonization rates, extinction rates, and survival of Northern Spotted Owls may all be negatively affected by the presence of Barred Owls in, or near, Northern Spotted Owl territories (Kelly et al. 2003, Olson et al. 2005, and Anthony et al. 2006).

Interspecific interference competition, expressed through aggressive physical contact between individuals (Morin 1999) could explain observed declines in occupancy, colonization, and survival of Northern Spotted Owls because of observed interactions between the two species (Dunbar et al. 1991 and Herter and Hicks 2000). Additionally, some anecdotal evidence suggests that occasionally these interactions may be lethal (Leskiw and Guiterrez 1998), and could represent the most extreme form of interference competition, intraguild predation. Intraguild predation occurs when the dominant of two morphologically similar species acts as both competitor and predator (Polis et al. 1989). In these instances, the dominant species benefits by the interaction through reducing competition for required resources, reducing risk to its offspring, and/or obtaining energetic benefits by consuming competitors (Sergio and Hiraldo 2008). Through direct lethal interaction, intraguild predation can greatly influence structure within top trophic communities by directly reducing components of the subordinate species' fitness. Several studies demonstrating that intraguild predation occurs in raptor communities that include owls (Sergio et al. 2003, Sergio et al. 2007, Martínez et al. 2008, Zuberogoitia et al. 2008) highlight the potential for intraguild predation on Northern Spotted Owls by Barred Owls. As a generalist and the larger of the two species, general theory regarding intraguild predation (Polis et al. 1989) predicts that Barred Owls should fill the role of dominant competitor and predator during interactions with Northern Spotted Owls. Northern Spotted Owl responsiveness to conspecific calls was reduced following exposure to Barred Owl calls (Crozier et al. 2006), providing additional support for the idea that Northern Spotted Owls may reduce their exposure to Barred Owls in areas of co-occurrence.

To determine whether interference competition is a plausible mechanism by which Barred Owls could be contributing to observed Northern Spotted Owl population declines, I conducted a series of playback experiments to elicit territorial responses from resident owls (see Chapter 1). In addition to broadcasting territorial vocalizations, I presented a life-sized taxidermy owl mount during experimental trials to mimic actual encounters in the wild as closely as possible. Through simulating inter- and intraspecific encounters and quantifying attack responses by territory residents, I attempted to determine whether or not interference competition by Barred Owls is a plausible mechanism by which Barred Owls could contribute to current Northern Spotted Owl population declines. Specifically, I investigated the “exclusion” and “acquiescence” hypotheses positing physical, aggressive interactions between the species as a mechanism by which Barred Owls could displace Northern Spotted Owls from their historic range. Under the “exclusion” hypothesis**,** Barred Owls actively exclude Northern Spotted Owls through interference competition expressed as frequent and rapid physical aggression with increased capacity to cause injury. Under the “acquiescence” hypothesis, Northern

Spotted Owls defend their territories less vigorously against Barred Owls than against Northern Spotted Owls as evidenced by lower levels of interspecific physical aggression relative to intraspecific aggression. To test both of these hypotheses, I investigated the overall frequency with which trials would result in an attack, the latency of strikes (i.e., rapidity of physical response) elicited by the simulated intruder, the total number of attacks directed at perceived intruders by the resident(s), and the capacity for the blunt force of strikes to cause injury to the intruder.

METHODS

The study area, experimental design, playback, and data collection procedures are described in detail in Chapter 1.

To quantify physical aggression, I categorized attacks as either strikes or swoops for analyses presented here. Strikes were defined as attacks in which direct contact between a resident owl and the taxidermy mount occurred. Swoops were instances in which a resident owl flew within 1m of the mount with its legs lowered but no physical contact occurred. Attacks were recorded with the use of two Sony camcorders. In addition to the infra-red lights built-in to the camcorders, four additional detachable infra-red lights were positioned around the trial site to improve the quality of the camcorder footage which was collected at night. Recorded footage was used to determine the time of attacks directed at the taxidermy mount and to distinguish swoops from occasions in which the resident flew past the mount but did not come within 1m or did not extend its legs.

To quantify the risk of head injury resulting from strikes, I recorded the accelerations experienced by the head of the owl mount as a result of strikes by resident owls. I placed a tri-axial analog accelerometer (PCB Piezotronics Model 356M162) into the head of the Northern Spotted and Barred Owl taxidermy mounts. To secure the accelerometer, the heads of the mounts were detached from the body, hollowed out, and a tube was fastened inside the head with epoxy. The accelerometer was then inserted into the hollow tube and secured in place with duct tape. The instrumented head was then replaced atop the taxidermy mount. A laptop computer powered the accelerometer through a signal conditioner (National Instruments NI USB-9162 with NI 9233 4 Channel Analogue Input). Acceleration data was recorded at a rate of 10,000 samples per second by the sensor, upon being "triggered" by an acceleration event, during strikes with the use of the LabView 8.5 Software package (National Instruments Corporation).

Data Analyses

Competing hypotheses were expressed as statistical models where attack code (i.e., occurrence of at least a single attack during the trial), strike latency, and total number of attacks were the modeled response variables (Table 2.1). Data analyses of these response variables followed the same procedures described in Chapter 1 where PROC LOGISTIC was used for logistic regression analyses to examine the binary response variable attack code (yes or no), and PROC GENMOD was used for linear regressions examining continuous response variables describing the magnitude of individuals' responses (i.e., strike latency and total number of attacks). As in Chapter 1, analyses were conducted on the entire data set and on data subsets consisting of data from trials where a response was detected and data from trials in which the number of years the residents had occupied the territory were known.

Injury Potential

The potential for brain injury resulting from strikes was compared using the Head Index Criterion (*HIC*) which is typically used in studies investigating human brain trauma (Turchi et al. 2004, Beckwith et al. 2007, Pfister et al. 2009). *HIC* was calculated over a period of 15 milliseconds (HIC_{15}) for all strikes because this time frame encapsulated the entire acceleration event recorded by the accelerometer for most strikes and has been used often in other studies on injury potential, particularly in humans (Jackson et al. 2002 and Pfister et al. 2009). HIC_{15} was calculated as:

$$HIC_{15} = \left[\frac{1}{(t_2 - t_1)} \int_{t_1}^{t_2} a(t)dt \right]^{2.5} (t_2 - t_1)$$

where $(t_2 - t_1) = .015\text{s}$ and $a(t)$ = the acceleration in g's occurring at time (t).

Mean HIC_{15} values, their standard errors, and 95% confidence intervals were calculated separately for strikes by each species to determine if an apparent difference in the risk of injury caused by blunt physical contact existed between these species.

To determine if the accelerometer output in the field accurately reflected the elastic collision theory (Appendix I) I created a pendulum with arm length of 154cm in a laboratory. The bob of the pendulum consisted of a variable number of metal washers, 6.2cm in diameter, lashed together and wrapped in felt. Accelerometer readings were obtained, using the same accelerometer, signal conditioner, and software utilized during the field portion of the study, from strikes directed at the head of the taxidermy mount with a bob weighing 131.2 and 211.0g. The different bob weights were chosen because they resulted in peak accelerations similar to those produced by resident owls that attacked during the playback trials (pers. obs.). Additionally, the ratio of the two bob weights (roughly 2:3) is similar to that of the ratio of male Northern Spotted Owl to female Barred Owl body masses (Mazur and James 2000). Pendulum trials were conducted with bobs of these two masses while elevating the bob to heights of 50.80 and 115.06cm. By varying the height to which the bob was raised, I was able to alter the velocity at which the bob struck the head of the owl mount (resulting in respective velocities of 1.0 and 1.50 m/s; which simulated two potential attacker velocities). Strikes were replicated 10 times at each combination of bob weight and height resulting in a total of 40 head strikes recorded. I then compared the effects of the different "attacker" masses and "attacker" velocities on HIC_{15} values.

RESULTS

One hundred and twenty-six playback trials were conducted in the 2008 and 2009 field seasons and used in the analyses presented here. One or more residents were detected during 34 of the 42 trials in which the Northern Spotted Owl treatment was presented in a Northern Spotted Owl territory. The male resident attacked the Northern Spotted Owl mount in nine of these trials and the number of male attacks elicited in single trial ranged from one to eight. One female Northern Spotted Owl resident attacked the Northern Spotted Owl mount once during a single trial. I conducted 45 trials where I presented the Barred Owl treatment to Northern Spotted Owl residents. Of the 45 trials, at least one resident responded in 32 of the trials. There was a single attack in one trial by the male resident, while the female resident attacked the Barred Owl mount in two trials with a total of one and nine attacks, respectively. The Northern Spotted Owl playback was presented in 39 Barred Owl territories. At least one resident responded in 19 of these trials. There were eight instances in which the male Barred Owl resident attacked the Northern Spotted Owl mount and no instances of the female attacking the owl mount were recorded. The total number of attacks by male Barred Owl residents elicited within a single trial ranged from one to six.

A larger proportion of trials conducted at Northern Spotted Owl territories were set-up within 100m of a last known location obtained during the daylight hours than for Barred Owls. Of 87 playback trials conducted at Northern Spotted Owl territories, only 14 (17%) were held at locations obtained between 9:00 PM and 4:00 AM PST. In comparison, 13 of 39 trials (33%) held within Barred Owl territories were conducted at locations obtained by field crews at night. The proclivity for Northern Spotted Owls to approach and perch within sight of the taxidermy mount prior to the initiation of the trial resulted in 26 of 87 (30%) total trials starting with one or more Northern Spotted Owls present. In contrast, none of the 37 trials conducted within Barred Owl territories began with a resident in sight. Although this discrepancy could potentially bias the strike latency response variable, I incorporated data from these trials in the analyses because the propensity for Northern Spotted Owls to investigate intruders would likely apply to potential competitors as well as humans.

Attack Code

Data from 126 trials were used to assess the likelihood of at least a single attack compared to no attack (attack code) by the male resident (Table 2.2). All models examined which contained the treatment variable (*TT*) had an Akaike weight >0, with no model having an Akaike weight >0.20 (Table 2.2). No variable other than *TT* was consistently found amongst the top-ranked models. Male Barred Owls presented with the Northern Spotted Owl treatment were more likely to attack the model ($\hat{\bar{\beta}} = 0.92$, 95% confidence interval (CI) = −0.18, 2.02; Table 2.3) than Northern Spotted Owls were to attack the Northern Spotted Owl treatment with 95% CI barely overlapping zero. Conversely, Northern Spotted Owls were less likely to attack the presented Barred Owl treatment than the Northern Spotted Owl treatment ($\hat{\bar{\beta}} = -1.82$, 95% CI = −3.51, −0.13; Table 2.3). Models having an Akaike weight >0 explained between 14 and 26% of the variation within the data (Table 2.2).

In models using the attack code at the territory level (response by the male and/or female), the adjusted Julian date (*AD*) variable was incorporated in four of the top five models, which had a cumulative Akaike weight of 0.76 (Table 2.4). Model-averaged estimates of the *AD* effect indicated a reduced likelihood of at least a single attack ($\hat{\bar{\beta}} = -0.03$, 95% CI= −0.05, −0.01) by either species over the season. Also, three of the top four models included reproductive code (*RC*) and together had an Akaike weight of 0.28. Model-averaged estimates of the *RC* effect suggested that breeding residents were slightly more likely to attack, with the 95% CI narrowly including zero ($\hat{\bar{\beta}} = 0.87$, 95% CI = −0.11, 1.84). Model-averaged estimates of the *TT* effect suggested that Barred Owls were as likely to attack when presented with the Northern Spotted Owl playback treatment as Northern Spotted Owls were ($\widehat{\bar{\beta}}$ = 0.27, 95% CI = −0.59, 1.14; Table 2.3) while Northern Spotted Owls appeared slightly less likely to attack the Barred Owl treatment than the Northern Spotted Owl treatment ($\widehat{\bar{\beta}}$ = −0.85, 95% CI = −1.87, 0.16; Table 2.3). The models tested at the territory level explained between 8 and 24% of the variation within these data (Table 2.4).

Responses from 79 playback trials were used to model the effect of *TT* on male attack code given that a male response was detected during the trial. *TT* and adjusted Julian date (*AD*) were present in the top two models which had a combined Akaike weight = 0.60 (Table 2.5). Model-averaged estimates of the effect size of *AD* suggested that male residents were less likely to attack as the season progressed ($\widehat{\bar{\beta}}$ = −0.03, 95% CI = −0.06, 0.01). Barred Owls were more likely to attack the Northern Spotted Owl model ($\widehat{\bar{\beta}}$ = 1.42, 95% CI = 0.25, 2.59; Table 2.6) and Northern Spotted Owls were less likely to attack the Barred Owl model ($\widehat{\bar{\beta}}$ = −2.02, 95% CI = −3.73, −0.31; Table 2.6) than Northern Spotted Owls receiving the Northern Spotted Owl treatment. Models with an Akaike weight >0 explained between 24 and 41% of the variation in the data (Table 2.5).

Models predicting attack code at the territory level for trials where a response was detected were analyzed using data from 86 playback trials. The top model included the *TT* and *AD* variables and had an Akaike weight (w_i = 0.80) considerably higher than the next best model (0.09). *AD* was present in the top four models (cumulative Akaike weight = 0.94; Table 2.7). The model-averaged estimate for *AD* was negative ($\widehat{\bar{\beta}}$ = −0.03, 95% CI = −0.06, −0.01) indicating that residents were less likely to attack later in the summer. The model-averaged estimate for the *TT* effect indicated that Barred Owl residents responded more to the Northern Spotted Owl treatment and Northern Spotted Owl residents responded less to the Barred Owl treatment when compared to trials where Northern Spotted Owls responded to conspecifics ($\hat{\bar{\beta}}$ = 0.88, 95% CI = −0.04, 1.79 and $\hat{\bar{\beta}}$ = −0.93, 95% CI = −1.86, 0.01 respectively; Table 2.6). The top model contained four parameters and explained 26% of the variation (Table 2.7).

Total Number of Attacks

Data from 126 trials were used to model the total number of attacks by male residents. The three top-ranked models all included *TT* and *AD* and collectively had an Akaike weight of 0.88 (Table 2.8). *AD* appeared to have little effect on the total number of attacks based on model-averaged estimates of the effect ($\hat{\bar{\beta}}$ = −0.02, 95% CI = −0.07, 0.03). Additionally, the female present variable (*FP*) appeared in the top two models (combined Akaike weight = 0.67), one of which was created *a posteriori*. The model-averaged effect of *FP* suggested that female presence had little effect on the total number of male attacks ($\hat{\bar{\beta}}$ = 1.05, 95% CI = −0.29, 2.39). Model-averaged estimates of *TT* effect size for trials simulating interspecific responses by Barred and Northern Spotted Owl residents suggested no differences from intraspecific responses by Northern Spotted Owls ($\hat{\bar{\beta}}$ = −1.10, 95% CI = −3.03, 0.84 and $\hat{\bar{\beta}}$ = −1.90, 95% CI = −4.81, 1.01 respectively; Table 2.3). The two best-ranked *a priori* models explained 17% of the variation in the data (Table 2.8).

The top four models predicting total number of attacks at the territory level (n = 126) included *AD* and collectively had an Akaike weight of 0.92 (Table 2.9). When the *AD* effect was averaged across models, the total number of attacks appeared to decline as the summer progressed ($\hat{\bar{\beta}}$ = −0.02, 95% CI = −0.04, 0.00). Reproductive behavior (*RC*) was also found in several of the top models (Table 2.9) and model-averaged estimates suggested that breeding residents attacked more often than non-breeders ($\hat{\bar{\beta}}$ = 1.52, 95% CI = −0.06, 3.10). Model-averaged estimates for the *TT* effect suggested no difference in the total number of attacks by either Barred or Northern Spotted Owl residents responding to the interspecific treatment compared to intraspecific trials in which Northern Spotted Owl residents were presented with the Northern Spotted Owl model ($\hat{\bar{\beta}}$ = −1.11, 95% CI = −3.09, 0.88 and $\hat{\bar{\beta}}$ = −1.11, 95% CI = −3.08, 0.86, respectively; Table 2.3). Models having an Akaike weight >0.10 explained between 13 and 18% of the variation in the data (Table 2.9).

Models predicting the total number of male attacks, given that a male response was detected, were evaluated with data from 79 playback trials. The *AD* variable indicated that number of attacks decreased as the summer progressed ($\hat{\bar{\beta}}$ = −0.03, 95% CI = −0.08, 0.01); it was included in the top three models (cumulative Akaike weight of 0.94; Table 2.10) and the 95% CI estimate narrowly included zero. Model-averaged parameter estimates for *TT* suggested that there was no difference for both interspecific treatment types relative to Northern Spotted Owl residents responding to the Northern Spotted Owl treatment ($\hat{\bar{\beta}}$ = −1.00, 95% CI = −3.13, 1.13 and $\hat{\bar{\beta}}$ = −2.65, 95% CI = −5.84, 0.54; Table 2.6).

The model set examining the total number of attacks at the territory level (male and female response combined), conditional upon a response by the male and/or female, was examined with data from 86 trials. The *AD* variable was included in the top four models which collectively held an Akaike weight of 0.95 (Table 2.11), but it had no apparent effect on the total number of attacks (model-averaged $\hat{\hat{\beta}} = -0.03$, 95% CI = −0.22, 0.17). Parameter estimates of the *TT* effect size suggested that there was no difference between treatments where Barred Owl residents were presented with the Northern Spotted Owl treatment and where Northern Spotted Owl residents were presented with the Barred Owl treatment relative to Northern Spotted Owl responses to conspecifics ($\hat{\hat{\beta}} = -0.69$, 95% CI's of −2.41, 1.02 and $\hat{\hat{\beta}} = -1.25$, 95% CI = −3.32, 0.81; Table 2.6).

Data from 84 playback trials, for which the number of years the male Northern Spotted Owl resident had occupied the territory was known, were used to assess behavioral plasticity in relation to duration of occupancy for the total number of male attacks. The number of years the male had occupied the territory (*MY*) failed to explain the total number of attacks observed, with no model including this covariate holding an Akaike weight greater than 0.01 (Table 2.12). When Akaike weights were normalized to include only models that contained the variable *MY* (i.e., an effect was assumed), model-averaged estimates did not suggest an effect ($\hat{\hat{\beta}} = 0.59$, 95% CI = −0.44, 1.62).

Eighty trials were used to evaluate whether the number of years a female had resided on the territory (*FY*) influenced the total number of female attacks. As with the analysis for the males, the models including *FY* did not account for much of the Akaike weight (cumulative Akaike weight = 0.10; Table 2.13). When Akaike weights were normalized, and an estimate for *FY* was calculated, there was little evidence for an effect ($\widehat{\widehat{\beta}}$ = 0.05, 95% CI = −0.06, 0.15). No covariates were effective in predicting the total number of female strikes in this analysis, with the intercept-only model having the greatest Akaike weight. The number of female strikes for the treatment where Northern Spotted Owl residents received the Barred Owl treatment did not differ from where Northern Spotted Owl residents were presented with the Northern Spotted Owl treatment ($\widehat{\widehat{\beta}}$ = 0.32, 95% CI of −0.46, 1.08; Table 2.6).

Of the three trials in which female Northern Spotted Owl residents attacked the presented owl mount, two of the trials involved the Barred Owl playback treatment. In comparison, of 10 trials resulting in at least one male Northern Spotted Owl attack, only one of the trials involved the Barred Owl playback treatment.

Strike Latency

I used data from 126 trials to estimate the effects on strike latencies, which were analyzed at the male and territory levels. Overall male strike latencies were poorly explained by variables other than *TT* and truncation code (*TC*); most models in the set received some Akaike weight (Table 2.14). The top models relating strike latency at the territory level incorporated either the variables *AD*, *RC*, or both (cumulative Akaike weight = 0.63; Table 2.18). However, model-averaged estimates suggested that these variables had little effect ($\widehat{\widehat{\beta}}$ = 0.03, 95% CI = −0.10, 0.16 for *AD*; $\widehat{\widehat{\beta}}$ = −9.49, 95% CI = −21.19, 2.21 for *RC*). Strike latencies were very similar at both the male and territory levels for trials in which Barred and Northern Spotted Owls were presented with the

Northern Spotted Owl treatment ($\hat{\bar{\beta}} = -0.24$, 95% CI = −5.33, 4.86 and $\hat{\bar{\beta}} = 1.04$, 95% CI = −4.15, 6.23, respectively; Table 2.3) and when Northern Spotted Owls were presented with the Barred Owl treatment ($\hat{\bar{\beta}} = 4.45$, 95% CI of −4.91, 13.80 for male only and $\hat{\bar{\beta}} = 3.02$, 95% CI = −3.84, 9.88 at the territory level; Table 2.3).

The *AD* variable was found in the top five models (cumulative Akaike weight of 0.71; Table 2.19) for the model set predicting male strike latency when a response was detected ($n = 79$ trials) but it appeared to have little effect (model-averaged $\hat{\bar{\beta}} = 0.09$, 95% CI = −0.33, 0.51). Given a male response, *TT* did not appear to have an effect on strike latency for either interspecific treatment when compared to the intraspecific treatment for Northern Spotted Owls ($\hat{\bar{\beta}} = -1.70$, 95% CI = −10.87, 7.46 for Barred Owl residents and $\hat{\bar{\beta}} = 7.34$, 95% CI = −7.70, 22.39 for Northern Spotted Owl residents; Table 2.6).

Results were similar for models examining strike latency at the territory level ($n = 86$ trials). Again, the *AD* variable was included in the top models (cumulative Akaike weight = 0.79; Table 2.17). Analysis of the effect of *AD* on strike latency provided weak evidence that residents were slower to strike as the season progressed ($\hat{\bar{\beta}} = 0.11$, 95% CI = −0.04, 0.26). Model-averaging the effect size of *TT* resulted in no apparent difference between treatments ($\hat{\bar{\beta}} = -2.46$, 95% CI = −10.52, 5.59 for Barred Owl residents receiving the Northern Spotted Owl treatment and $\hat{\bar{\beta}} = 3.62$, 95% CI = −4.60, 11.83 for trials in which Northern Spotted Owls received the Barred Owl treatment; Table 2.6).

HIC_{15} Values

Strike data were collected during the spring and summer field seasons in 2009. In total, 8 instances of Barred Owls striking the Northern Spotted Owl taxidermy mount collected from 5 individuals and 14 instances of Northern Spotted Owls striking the Northern Spotted Owl mount from 2 individuals were used to compare HIC_{15} values across species. HIC_{15} estimates ranged from 35.80 to 83.33 ($\bar{x}$ = 57.42, 95% CI = 45.86, 68.98) for Barred Owl strikes and 26.92 to 318.24 ($\bar{x}$ = 113.61, 95% CI = 74.04, 153.18) for Northern Spotted Owl strikes (Table 2.18).

Results of the 40 pendulum strikes showed that a 50% increase in body mass (131.7 to 211.0 g) with bob velocity remaining constant equates to HIC_{15} increases of 64% at a velocity of 1.0 m/s and 18% at 1.5 m/s (Table 2.19). In contrast, increasing velocity by 50% (from 1 to 1.5 m/s) results in HIC_{15} increases of 400% when the bob mass was 131.7g and 257% when the bob mass was 211g (Table 2.20). These results agree with the general principle of the elastic collision equation (see Appendix I for additional details), and indicate that attacker flight velocity has a substantially greater influence on the injury potential caused by head acceleration during strikes than does attacker body mass.

Summary of Results

Overall, results of this study provided mixed support for the “exclusion” and “acquiescence” hypotheses (Table 2.21). Barred Owls attacked the Northern Spotted Owl mount more frequently than Northern Spotted Owls which supported the predictions of the “exclusion” hypothesis; however, the reduced number of overall attacks by Barred Owls compared to Northern Spotted Owls and similar strike latencies among treatments did not. The “acquiescence” hypothesis was fairly well supported by the results, with Northern Spotted Owls attacking the Barred Owl treatment less frequently and fewer times overall compared to the Northern Spotted Owl treatment. Results of the strike latency analyses which predicted latencies to be greater for Northern Spotted Owls receiving the Barred Owl treatment did not support the “acquiescence” hypothesis; however, as no difference was detected among treatments.

The potential for injury resulting from acceleration of the victim’s head was greater during strikes by Northern Spotted Owls than by Barred Owls, which did not support either the “exclusion” or “acquiescence” hypotheses. Together, the results of the elastic collision calculations (Appendix I) and data collected in the laboratory with a pendulum indicate that Northern Spotted Owls’ ability to strike with an increased capacity to cause injury is likely related to increased flight velocity.

DISCUSSION

General Considerations

Attacks by residents were recorded during one or more trials of all three treatment types. In general, male residents attacked the presented owl mount far more frequently than females; however, female Northern Spotted Owls did attack the Barred Owl mount on two occasions compared to a single instance of a male Northern Spotted Owl attacking the Barred Owl treatment. Attack rates declined markedly throughout the summer season indicating that spring to early summer is primarily when intra- and interspecific physical aggression takes place in this system. Additionally, breeding females may be more likely to engage in physical altercations than non-breeders.

“Acquiescence” Hypothesis

I found strong support for the “acquiescence” hypothesis with both attack frequency and total number of attacks, yet there was a lack of a treatment effect for strike latency (Table 2.21). Northern Spotted Owl residents attacked the Barred Owl treatment less frequently and had fewer attacks than when they encountered the Northern Spotted Owl treatment. Thus, Northern Spotted Owls appeared less likely to attack Barred Owls than they are conspecifics.

Martínez et al. (2008) found that dominance in intra- and interspecific interactions is primarily determined by body mass in raptor assemblages, with larger individuals assuming the dominant role. The results of my study agree with this generalization: the smaller Northern Spotted Owl struck the Barred Owl mount less frequently than they struck the Northern Spotted Owl treatment.

In the most extreme form of interference competition, intraguild predation (see Polis et al. 1989), Mikkola (1976) found that smaller owls were occasionally in diets of larger owls but the reverse almost never occurred. Mikkola (1976) also demonstrated that generalist owls engaged in intraguild predation far more frequently, presumably because they could gain energetic benefits from the consumption of a competitor. As Northern Spotted Owls are considered prey specialists, they are unlikely to attack congenerics for potential energetic gains associated with predation.

The observed lower level of intensity of physical response by Northern Spotted Owls may stem from a combination of lighter body mass, higher levels of trophic specialization, or may have evolved to avoid potential predation from larger owls by reducing the frequency of physical altercations. Thus, Northern Spotted Owls do not physically defend their territories against Barred Owls as vigorously as they do against conspecifics. Relatively lower levels of physical aggression by Northern Spotted Owls suggest that this species may assume the role of subordinates when interspecific encounters with Barred Owls do occur.

Strike latency was particularly variable among trials as demonstrated by the large confidence intervals for the treatment effect. Two aspects of this study may have influenced this variability. First, nearly twice as many trials conducted at Barred Owl territories were held at locations where the residents had been detected at night compared to trials conducted at Northern Spotted Owl territories. These trials may have been held farther from the residents' territory center, potentially resulting in more time elapsing between the start of the trial and the residents' first detecting the treatment. Additionally, Northern Spotted Owl residents were present at the trial site when the trial started during nearly $^1/_3$ of the trials held at Northern Spotted Owl territories. Northern Spotted Owls present at the onset of the trial were certainly able to detect the treatment immediately. In contrast, Barred Owl residents were never present at the beginning of the trial, and may have had more time elapse between the start of the trial and the moment when they first detected the treatment.

The results from the physical aggression analyses indicating that Northern Spotted Owls are likely to act as subordinates during interspecific interactions with Barred Owls agree with the findings discussed in Chapter 1 of this thesis: Northern Spotted Owls called less frequently when presented with the Barred Owl treatment than the Northern Spotted Owl treatment. Although Northern Spotted Owls responded with similar frequency to both intra- and interspecific treatments, the combination of reduced magnitudes of vocal and physical aggression during interspecific conflicts indicate that when interspecific encounters do occur Northern Spotted Owls are more likely to yield to the larger Barred Owl, in support of the "acquiescence" hypothesis.

"Exclusion" Hypothesis

The "exclusion" hypothesis was supported in this study by male Barred Owls attacking the Northern Spotted Owl mount more frequently when they responded to the treatment than Northern Spotted Owls attacked conspecifics. However, there was no difference in either strike latencies or total number of attacks providing no support for the "exclusion" hypothesis which predicts that Barred Owl strike latencies would be lower and the total number of attacks would be greater than these values would be for Northern Spotted Owls.

The increased frequency with which Barred Owl residents attacked the model is consistent with past research that found dominance in interspecific interactions was generally related to body mass (Martínez et al. 2008). Because Barred Owls are the larger of the two species, their dominance in interactions with smaller Northern Spotted Owls is consistent with this idea. Attacks by Barred Owls could result in Northern Spotted Owl mortality (Leskiw and Gutiérrez 1998), which might explain the observed reduction of Northern Spotted Owl survival in the presence of Barred Owls (Anthony et al. 2006). In Europe, Ural Owls (*Strix uralensis)* occasionally prey upon the slightly smaller Eurasian Tawny Owl (*Strix aluco)* (Mikkola 1976), further supporting the idea that slightly larger *Strix* spp. depredate smaller congenerics. During predation, the predator can benefit from both energetic gains associated with eating their prey and a reduction in competition over shared resources (Polis et al. 1989). Effects of even occasional intraguild predation can extend beyond the direct lethal effects to the individual, ultimately affecting the population and community levels. Behavioral changes stemming from predator avoidance can lower fitness by effectively reducing available habitat, through changes in foraging behavior, and by reducing the ability of individuals to find mates and hold territories (Lima and Dill 1990, Hakkarainen and Korpimäki 1996, Sergio et al. 2007).

The number of attacks by Barred Owl residents that I was able to document may have been greater if this species was less sensitive to human disturbance. When I approached the taxidermy mount to replace its head following the first strike, Barred Owls would fly to the upper canopy, where they would often stay for the remainder of the trial. In contrast, Northern Spotted Owls would often fly in to the trial site and perch nearby while we were setting up. Following the first strike, Northern Spotted Owls would retreat only a short distance and occasionally attacked the mount again even while I was in the process of replacing the mount’s head. It has been suggested that Northern Spotted Owls are not disturbed by human presence because they have been habituated to humans who frequently provide mice during surveys (“mousing” technique described in Lint et al. 1999). Because I witnessed unbanded Northern Spotted Owls, that presumably had never been “moused,” behaving in this manner, I believe that this is not a learned behavior, but an innate difference between these species. Differences in response to human disturbance by these two species would explain the similar total number of attacks by Barred Owls throughout the study despite attacks occurring in a greater number of trials.

The "exclusion" hypothesis predicts that Barred Owls receiving the Northern Spotted Owl treatment would have lower strike latencies than Northern Spotted Owls striking conspecifics. This prediction was not supported by the results of this study. Overall, strike latencies for all treatments proved to be highly variable, resulting in large confidence intervals and a high degree of uncertainty in estimates of the *TT* effect. The differences in the proportion of trials conducted at locations obtained during the day and night-time for the two species' may be partially responsible for this variability, because it is more likely that the treatment would be detected by the residents when trials were conducted at day-time (roost) locations within the core area of the residents' territory as opposed to night-time (foraging) locations. Also, the propensity of Northern Spotted Owls to be within sight of the mount at the onset of the trial (as previously described) may have contributed to this variability.

Overall, the Barred Owls' striking the Northern Spotted Owl mount more frequently than Northern Spotted Owls indicates that Barred Owls are likely to act as dominants during interspecific interactions and agrees with the findings from Chapter 1, in which Barred Owls called more frequently while responding to the Northern Spotted Owl treatment than Northern Spotted Owls.

HIC$_{15}$

Data obtained in the field suggest that Northern Spotted Owls exhibit a greater potential to cause head trauma resulting from blunt force than do Barred Owls. Attacker flight velocity immediately prior to impact appears to have a larger effect on the resultant head acceleration following a strike than does attacker body mass. As a smaller and presumably more maneuverable species, it seems likely that Northern Spotted Owls are able to reach greater flight velocities than Barred Owls in the confined understory of the forest types where trials took place. Another potential explanation for the differences in HIC_{15} values recorded for these two species is that Northern Spotted Owl residents may have struck the presented owl mount's head more directly, while Barred Owl residents delivered glancing blows, during the relatively few samples recorded in the field. Despite this possibility, my findings from the data recorded contradict both the "exclusion" and "acquiescence" hypotheses which predicted that strikes from the larger Barred Owl would result in greater HIC_{15} values. However, it is still unclear whether the HIC_{15} values observed in this study could prove lethal for either Northern Spotted or Barred Owls.

HIC_{15} assesses the potential for human brain injury caused by head acceleration due to blunt physical contact and fails to account for potential puncture or laceration injuries inflicted by talons. One study investigating the amount of force raptors are capable of applying with their talons found that grip force increased exponentially with body mass (Ward et al. 2002). As Barred Owl males typically have similar body masses to female Northern Spotted Owls (Mazur and James 2000), differences in grip force would likely be more evident in interspecific interactions involving male Northern

Spotted Owls and in interspecific interactions between females. It is possible that injuries resulting from puncture wounds and lacerations may allow Barred Owls to inflict potentially mortal wounds, a factor that my study did not evaluate. The question still remains as to whether Barred Owls have a greater ability to inflict injury with their talons during aggressive physical contact and, hence, the ability to cause lethal injuries to Northern Spotted Owls.

Effect of Covariates

Duration of Territory Occupancy (MY and FY)

The number of attacks directed at the playback treatment was not influenced by the covariate for the number of years the males or females had occupied territories. Although a study on Song Sparrow territoriality demonstrated increased levels of territorial defense by individuals with more experience on the territory (Hyman et. al. 2004), the lack of an effect in my study suggests that the advantages gained by Northern Spotted Owls from experience residing in a territory (i.e., knowledge of terrain, territorial borders, and location of prey) may be obtained within a single season or do not affect the degree of territoriality in Northern Spotted Owls.

Seasonality (AD)

The probability that an owl would attack the model decreased as the season progressed. This suggests that physical aggression plays a more prominent role in territorial behavior during the spring and early summer compared to other parts of the breeding season, and this behavior likely promotes territory retention when faced with potential competitors. The increased levels of physical aggression may be a result of higher levels of particular hormones early in the breeding season. For instance, testosterone has been shown to affect aggressiveness in numerous avian species (Balthazart 1983, Hunt et al. 1997), with levels typically declining as the season progresses when parents begin to feed young (Wingfield et al. 1990 and Wingfield and Farner 1993).

Breeding Behavior (RC)

The frequency and total number of attacks were higher among residents known to be breeding compared to residents that were not breeding during the season at the territory level. Because *RC* was not an important variable in the analyses of response variables for the male resident, it appears that breeding status has a greater influence on female territorial defense behavior in Northern Spotted Owls. These results are consistent with past research. For instance, female long-eared owls play a more prominent role in nest defense than do males, as exhibited through increased frequency of aggressive calling and more frequent physical defense of nest (swooping at threats to nest, broken-wing displays, and assuming threatening postures) (Galeotti et al. 2000). Additionally, female Ural Owls, members of the *Strix* genus, which defended their nests and young more vigorously had more offspring survive to reproduce (Kontiainen et al. 2009). These studies indicate that females that aggressively respond to perceived threats to their young can obtain direct fitness benefits through this behavior and offer a plausible explanation for the observed effect of breeding behavior in my study.

Implications for Managers

The intensity of vocal (Chapter 1) and physical interactions between Barred and Northern Spotted Owls witnessed in my study suggest that Barred Owls may act as dominants when these two species engage in territorial conflict. Amarasekare (2002) suggested that exclusion of a native species by an invasive species is likely if the invasive species exerts dominance in interspecific interference competition and if it is superior at exploiting resources. Barred Owls are generalist predators that can exist at higher densities than Northern Spotted Owls (Hamer et al. 2007), indicating that they are superior at resource exploitation. The presumed dominant role that Barred Owls exert, which was suggested by my study, coupled with the apparent increased ability to exploit resources, fits the scenario that Amarasekare (2002) suggests will ultimately result in exclusion. Therefore, competitive exclusion appears to be a plausible explanation for the numerous observational and correlative studies indicating that Barred Owls have negative effects on Northern Spotted Owls (Kelly et al. 2003, Olson et al. 2005, Anthony et al. 2006).

Although displacement of Northern Spotted Owls by Barred Owls appears to be the most likely outcome of the Barred Owl range expansion, viable populations of Northern Spotted Owls may persist under a number of scenarios. Overall, residents' responses to the playback were highly variable and indicate a substantial degree of behavioral plasticity among individuals. This plasticity might result from heritable genetic differences among Northern Spotted Owls. If aggression is a heritable trait, intense intraspecific competition among Northern Spotted Owls for high-quality habitat could potentially result in aggressive individuals occupying the most productive territories. By preserving high-quality Northern Spotted Owl habitat, managers may, in effect, select for these aggressive individuals assuming residents of these high-quality sites produce offspring that are recruited into the population. Subsequent changes in genetic structure at the population level could then increase the territory holding potential of Northern Spotted Owls in the presence of Barred Owls over time.

Additionally, changes in individual behavior as a result of learning may mitigate some risk to Northern Spotted Owls. Predator avoidance usually occurs in the form of temporal segregation, risk-sensitive habitat selection, spatial avoidance, and/or short-term behavioral avoidance (Sergio and Hiraldo 2008). Temporal segregation is not plausible because these two species are primarily nocturnal. However, these two species do exhibit some differences in habitat preference (Herter and Hicks 2000, Pearson and Livezey 2003, Hamer et al. 2007), making risk-sensitive habitat selection and spatial avoidance possible. To determine if risk-sensitive habitat selection or spatial avoidance of Barred Owls could allow Northern Spotted Owls to persist, managers should seek to determine if areas where Barred Owls are currently absent (i.e., higher elevation sites, more xeric areas, and regions with steeper slopes) can facilitate sufficient survival and fecundity to allow for viable Northern Spotted Owl populations. Also, Northern Spotted Owls may learn to exhibit short-term behavioral avoidance to reduce the frequency of agonistic interactions with Barred Owls. Results from Crozier et al. 2006 indicate that this might already be occurring in some areas of co-existence, with Northern Spotted Owls calling less frequently in the presence of Barred Owls and subsequently decreasing the rate at which Barred Owls detect these individuals.

Finally, the persistence of Northern Spotted Owls could be aided by Barred Owl removal in areas where these two species co-occur. Unfortunately, lethal control represents both the most cost-effective and practical form of removal in this instance (Gutiérrez et al. 2007). Although this strategy is unpalatable among the public, political, and scientific communities alike (Gutiérrez et al. 2007), it is not without precedent in recovery efforts for threatened and endangered species (Courchamp et al. 2003).

In conclusion, results of this study suggest that interspecific interference competition is likely to occur with Barred Owls assuming the role of dominants during interactions. Therefore, long-term conservation of the Northern Spotted Owl will likely depend upon behavioral shifts by Northern Spotted Owls to reduce competition in the presence of Barred Owls over time, plasticity in territorial aggressiveness by Northern Spotted Owls, the existence of refugia within the current Northern Spotted Owl's range affording habitat-mediated or distance-sensitive avoidance, or the active management of Barred Owl populations to conserve Northern Spotted Owls.

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Table 2.1. Description of response variables used in analyses of data from experimental playback trials on Barred and Northern Spotted Owls conducted in northwestern California.

Response Variable	Variable Type	Description
Male Attack Code	Categorical	Whether a male attacked (1) or did not attack (0) the presented mount during the trial
Total Number of Male Attacks	Continuous	Total number of male strikes and swoops during the trial
Male Strike Latency	Continuous	# of minutes from the start of the trial to the first strike directed at the presented mount by the male
Male and Female Attack Code	Categorical	Whether the male and/or female attacked (1) or did not attack (0) the presented mount during the trial
Total Number of Male and Female Attacks	Continuous	Total number of male and/or female strikes and swoops during the trial
Male and Female Strike Latency	Continuous	# of minutes from the start of the trial to the first strike directed at the presented model by the male or female
Total Number of Female Attacks	Continuous	Total number of female strikes and swoops during the trial

Table 2.2. Ranking of *a priori* and *a posteriori* models used to analyze male Barred and Northern Spotted Owl attack code (yes or no response) for 126 experimental playback trials conducted in northwestern California. AICc is a small sample size correction factor for AIC. ΔAICc is the difference in AICc units between a given model and the top-ranking model. Akaike weight is the probability that a given model is the best-approximating model of the models tested. Covariates included in the models are described in Table 1.5.

Model	R^2	**K**	**AIC**	**AICc**	**ΔAICc**	**Akaike Weight**
TT + AD	0.20	4	96.11	96.44	0.00	0.20
TT + FP + AD + FP*AD	0.25	6	96.22	96.92	0.48	0.16
TT + FP	0.20	4	96.75	97.08	0.64	0.14
TT + TC	0.18	4	97.91	98.24	1.80	0.08
TT + RC	0.21	5	97.87	98.37	1.93	0.08
TT + AD + FP + TT*AD[†]	0.26	7	97.61	98.56	2.12	0.07
TT	0.14	3	98.82	99.01	2.57	0.06
TT + YC	0.16	4	99.37	99.70	3.26	0.04
TT+ UD	0.16	4	99.41	99.74	3.30	0.04
TT + AD + TT*AD	0.22	6	99.09	99.79	3.35	0.04
TT + SC	0.16	4	99.50	99.83	3.38	0.04
TT + RC + AD + RC*AD	0.26	8	99.56	100.79	4.35	0.02
TT + RC + FP + RC*FP	0.26	8	99.65	100.88	4.44	0.02
TT + EM	0.14	4	100.80	101.13	4.69	0.02
Intercept Only	0.00	1	105.35	105.38	8.94	0.00

[†] *a posteriori* model

Table 2.3. Model-averaged estimates and 95% confidence intervals for treatment effects for the treatment types, Barred Owl residents presented with Northern Spotted Owl treatment (BAOW/SPOW) and Spotted Owl residents presented with Barred Owl treatment (SPOW/BAOW), relative to trials in which Northern Spotted Owl residents were presented with the Northern Spotted Owl treatment (SPOW/SPOW) ($n = 126$).

	BAOW/SPOW Treatment†		**SPOW/BAOW Treatment†**	
Model Set	**Estimate**	**95% CI**	**Estimate**	**95% CI**
For All Trials				
Male Attack Code	0.92	−0.18, 2.02	−1.82	−3.51, −0.13
Male and Female Attack Code	0.27	−0.59, 1.14	−0.85	−1.87, 0.16
Total Number of Male Attacks	−1.1	−3.03, 0.84	−1.90	−4.81, 1.01
Total Number of Male and Female Attacks	−1.11	−3.09, 0.88	−1.11	−3.08, 0.86
Male Strike Latency	−0.24	−5.33, 4.86	4.45	−4.91, 13.80
Male and Female Strike Latency	1.04	−4.15, 6.23	3.02	−3.84, 9.88

†For each treatment type, the first 4-letter AOU code listed represents the resident species followed by the playback species that was presented.

Table 2.4. Ranking of *a priori* and *a posteriori* models used to analyze territory attack code response by Barred and Northern Spotted Owls for 126 experimental playback trials conducted in northwestern California. AICc is a small sample size correction factor for AIC. ΔAICc is the difference in AICc units between a given model and the top-ranking model. Akaike weight is the probability that a given model is the best-approximating model of the models tested within the model set. Covariates included in the models are described in Table 1.5.

Model	R^2	**K**	**AIC**	**AICc**	**ΔAICc**	**Akaike Weight**
TT + AD	0.17	4	108.25	108.58	0.00	0.48
TT + RC + AD + RC*AD	0.24	8	110.33	111.56	2.97	0.11
TT + RC + AD + TT*AD[†]	0.24	8	110.36	111.59	3.00	0.11
TT + RC	0.15	5	111.91	112.41	3.82	0.07
TT + AD + TT*AD	0.17	6	111.77	112.48	3.89	0.07
TT + UD	0.10	4	113.55	113.88	5.29	0.03
TT	0.08	3	113.73	113.93	5.34	0.03
TT + TC	0.10	4	113.74	114.07	5.48	0.03
TT + YC	0.10	4	113.96	114.29	5.71	0.03
Intercept Only	0.00	1	115.54	115.57	6.99	0.01
TT + SC	0.08	4	115.34	115.67	7.08	0.01
TT + EM	0.08	4	115.63	115.96	7.38	0.01

[†] *a posteriori* model

Table 2.5. Ranking of *a priori* models used to analyze male attack code by Barred and Northern Spotted Owls, conditional upon a male response, for 79 experimental playback trials conducted in northwestern California. AICc is a small sample size correction factor for AIC. ΔAICc is the difference in AICc units between a given model and the top-ranking model. Akaike weight is the probability that a given model is the best-approximating model of the models tested within the model set. Covariates included in the models are described in Table 1.5.

Model	R^2	**K**	**AIC**	**AICc**	**ΔAICc**	**Akaike Weight**
TT + AD	0.35	4	72.41	72.95	0.00	0.51
TT + AD + TT*AD	0.36	6	75.14	76.30	3.35	0.09
TT + TC	0.29	4	75.79	76.33	3.37	0.09
TT + RC	0.32	5	76.43	77.25	4.30	0.06
TT + FP + AD + FP*AD	0.35	6	76.39	77.56	4.60	0.05
TT	0.24	3	77.46	77.78	4.82	0.05
TT + RC + AD + RC*AD	0.41	8	75.89	77.95	4.99	0.04
TT + YC	0.25	4	78.39	78.93	5.97	0.03
TT + UD	0.25	4	78.46	79.00	6.04	0.02
TT + SC	0.25	4	78.66	79.20	6.24	0.02
TT + FP	0.24	4	79.08	79.62	6.67	0.02
TT + EM	0.24	4	79.30	79.84	6.88	0.02
TT + RC + FP + RC*FP	0.32	8	81.92	83.98	11.03	0.00
Intercept Only	0.00	1	86.79	86.84	13.89	0.00

Table 2.6. Model-averaged estimates and 95% confidence intervals for treatment effects of Barred Owl residents presented with Northern Spotted Owl treatment (BAOW/SPOW) and Spotted Owl residents presented with Barred Owl treatment (SPOW/BAOW) relative to trials in which Northern Spotted Owl residents were presented with the Northern Spotted Owl treatment (SPOW/SPOW).

	BAOW/SPOW Treatment†		**SPOW/BAOW Treatment†**	
Model Set	**Estimate**	**95% CI**	**Estimate**	**95% CI**
***For Trials with a Male Response* (*n* = 79)**				
Male Attack Code	1.42	0.25, 2.59	−2.02	−3.73, −0.31
Total Number of Male Attacks	−1.00	−3.13, 1.13	−2.65	−5.84, 0.54
Male Strike Latency	−1.70	−10.87, 7.46	7.34	−7.70, 22.39
***For Trials with a Male and/or Female Response* (*n* = 86)**				
Male and Female Attack Code	0.88	−0.04, 1.79	−0.93	−1.86, 0.01
Total Number of Male and Female Attacks	−0.69	−2.41, 1.02	−1.25	−3.32, 0.81
Male and Female Strike Latency	−2.46	−10.52, 5.59	3.62	−4.60, 11.83
For Trials where # of Years Spent on Territory was available				
Total Number of Male Attacks **(*n* = 84)**	—§	—§	−2.24	−5.38, 0.91
Total Number of Female Attacks **(*n* = 80)**	—§	—§	0.32	−0.45, 1.08

†For each treatment type, the first 4-letter AOU code listed represents the resident species followed by the playback species that was presented.

§ Data not available for analysis

Table 2.7. Ranking of *a priori* and *a posteriori* models used to analyze territory attack code by Barred and Northern Spotted Owls, conditional upon a male and/or female response, for 86 experimental playback trials conducted in northwestern California. AICc is a small sample size correction factor for AIC. ΔAICc is the difference in AICc units between a given model and the top-ranking model. Akaike weight is the probability that a given model is the best-approximating model of the models tested. Covariates included in the models are described in Table 1.5.

Model	R^2	**K**	**AIC**	**AICc**	**ΔAICc**	**Akaike Weight**
TT + AD	0.26	4.00	87.43	87.92	0.00	0.80
TT + AD + TT*AD	0.26	6.00	91.29	92.35	4.43	0.09
TT + RC + AD + RC*AD	0.30	8.00	92.61	94.48	6.55	0.03
TT + RC + AD + TT*AD†	0.29	8.00	93.21	95.08	7.16	0.02
TT + UD	0.12	4.00	96.10	96.59	8.67	0.01
TT	0.09	3.00	96.33	96.62	8.70	0.01
TT + TC	0.12	4.00	96.33	96.82	8.90	0.01
TT + YC	0.12	4.00	96.47	96.96	9.04	0.01
Intercept Only	0.00	1.00	97.61	97.65	9.73	0.01
TT + RC	0.14	5.00	97.12	97.87	9.95	0.01
TT + SC	0.09	4.00	98.02	98.51	10.59	0.00
TT + EM	0.09	4.00	98.31	98.80	10.88	0.00

† *a posteriori* model

Table 2.8. Ranking of *a priori* and *a posteriori* models used to analyze the total number of male attacks by Barred and Northern Spotted Owls for 126 experimental playback trials conducted in northwestern California. AICc is a small sample size correction factor for AIC. ΔAICc is the difference in AICc units between a given model and the top-ranking model. Akaike weight is the probability that a given model is the best-approximating model of the models tested. Covariates included in the models are described in Table 1.5.

Model	R^2	**K**	**AIC**	**AICc**	**ΔAICc**	**Akaike Weight**
TT + FP + AD + FP*AD	0.17	7	475.95	476.90	0.00	0.34
TT + AD + FP + TT*AD[†]	0.19	8	475.76	476.99	0.09	0.33
TT + AD + TT*AD	0.17	7	476.97	477.92	1.02	0.21
TT + AD	0.12	5	479.95	480.45	3.56	0.06
TT + FP	0.10	5	482.14	482.64	5.75	0.02
TT + FP + TT*FP	0.13	7	482.57	483.52	6.63	0.01
TT	0.08	4	484.21	484.54	7.65	0.01
TT + RC + AD + RC*AD	0.15	9	483.66	485.21	8.32	0.01
TT + RC	0.10	6	484.68	485.39	8.49	0.00
TT + UD	0.08	5	485.46	485.96	9.07	0.00
TT + YC	0.08	5	485.82	486.32	9.42	0.00
TT + EM	0.08	5	486.13	486.63	9.73	0.00
TT + SC	0.08	5	486.14	486.64	9.74	0.00
TT + PC	0.08	6	487.09	487.80	10.90	0.00
TT + RC + FP + RC*FP	0.13	9	486.96	488.51	11.61	0.00
Intercept Only	0.00	2	490.09	490.19	13.30	0.00
TT + RC + RC*TT	0.13	10	488.64	490.55	13.66	0.00

[†] *a posteriori* model

Table 2.9. Ranking of *a priori* and *a posteriori* models used to analyze total number of male and female attacks by Barred and Northern Spotted Owls for 126 experimental playback trials conducted in northwestern California. AICc is a small sample size correction factor for AIC. ΔAICc is the difference in AICc units between a given model and the top-ranking model. Akaike weight is the probability that a given model is the best-approximating model of the models tested. Covariates included in the models are described in Table 1.5.

Model	R^2	**K**	**AIC**	**AICc**	**ΔAICc**	**Akaike Weight**
TT + RC + AD + RC*AD	0.18	9	502.68	504.24	0.00	0.34
TT + AD	0.11	5	504.21	504.71	0.48	0.26
TT + RC + AD + TT*AD†	0.17	9	503.75	505.31	1.07	0.20
TT + AD + TT*AD	0.13	7	505.42	506.37	2.14	0.12
TT + TC	0.09	5	507.66	508.16	3.92	0.05
TT + RC	0.09	6	509.85	510.55	6.32	0.01
TT	0.04	4	511.49	511.82	7.58	0.01
TT + UD	0.05	5	512.84	513.34	9.11	0.00
Intercept Only	0.00	2	513.26	513.35	9.12	0.00
TT + SC	0.05	5	513.18	513.68	9.44	0.00
TT + YC	0.05	5	513.45	513.95	9.72	0.00
TT + EM	0.04	5	513.46	513.96	9.73	0.00
TT + PC	0.05	6	514.45	515.15	10.92	0.00
TT + RC + RC*TT	0.10	10	516.41	518.33	14.09	0.00

† *a posteriori* model

Table 2.10. Ranking of *a priori* models used to analyze total number of male attacks by Barred and Northern Spotted Owls, conditional upon a male response, for 79 experimental playback trials conducted in northwestern California. AICc is a small sample size correction factor for AIC. ΔAICc is the difference in AICc units between a given model and the top-ranking model. Akaike weight is the probability that a given model is the best-approximating model of the models tested. Covariates included in the models are described in Table 1.5.

Model	R^2	**K**	**AIC**	**AICc**	**ΔAICc**	**Akaike Weight**
TT + AD + TT*AD	0.25	7	328.55	328.86	0.00	0.65
TT + AD	0.18	5	330.74	330.96	2.10	0.23
TT + FP + AD + FP*AD	0.20	7	333.41	333.72	4.87	0.06
TT	0.10	4	336.79	336.97	8.11	0.01
TT + RC + AD + RC*AD	0.20	9	336.92	337.33	8.47	0.01
TT + FP	0.11	5	337.56	337.78	8.92	0.01
TT + RC	0.13	6	338.07	338.34	9.48	0.01
TT + UD	0.10	5	338.17	338.39	9.54	0.01
TT + YC	0.10	5	338.62	338.84	9.98	0.00
TT + SC	0.10	5	338.73	338.95	10.10	0.00
TT + EM	0.10	5	338.75	338.97	10.11	0.00
TT + FP + TT*FP	0.13	7	339.94	340.25	11.40	0.00
TT + PC	0.11	6	340.07	340.33	11.48	0.00
Intercept Only	0.00	2	340.86	340.95	12.10	0.00
TT + RC + FP + RC*FP	0.14	9	342.80	343.20	14.35	0.00
TT + RC + RC*TT	0.16	10	343.33	343.78	14.93	0.00

Table 2.11. Ranking of *a priori* and *a posteriori* models used to analyze total number of male and female attacks by Barred and Northern Spotted Owls, conditional upon one or more residents responding, for 86 experimental playback trials conducted in northwestern California. AICc is a small sample size correction factor for AIC. ΔAICc is the difference in AICc units between a given model and the top-ranking model. Akaike weight is the probability that a given model is the best-approximating model of the models tested. Covariates included in the models are described in Table 1.5.

Model	R^2	**K**	**AIC**	**AICc**	**ΔAICc**	**Akaike Weight**
TT + AD	0.17	5	369.90	370.10	0.00	0.56
TT + RC + AD + RC*AD	0.22	9	372.56	372.93	2.83	0.14
TT + AD + TT*AD	0.18	7	372.66	372.94	2.84	0.14
TT + RC + AD + TT*AD†	0.22	9	372.94	373.31	3.21	0.11
TT + TC	0.11	5	375.93	376.13	6.03	0.03
TT + RC	0.10	6	378.90	379.14	9.04	0.01
TT	0.05	4	379.67	379.83	9.73	0.00
Intercept Only	0.00	2	379.83	379.92	9.82	0.00
TT + UD	0.05	5	381.13	381.33	11.23	0.00
TT + SC	0.05	5	381.45	381.65	11.55	0.00
TT + YC	0.05	5	381.63	381.83	11.74	0.00
TT + EM	0.05	5	381.65	381.85	11.75	0.00
TT + PC	0.05	6	383.05	383.29	13.19	0.00
TT + RC + RC*TT	0.11	10	385.58	386.00	15.90	0.00

† *a posteriori* model

Table 2.12. Ranking of *a priori* and *a posteriori* models used to analyze the effect of duration of occupancy on total number of male attacks by Barred and Northern Spotted Owls for 84 playback experimental playback trials conducted in northwestern. AICc is a small sample size correction factor for AIC. ΔAICc is the difference in AICc units between a given model and the top-ranking model. Akaike weight is the probability that a given model is the best-approximating model of the models tested. Covariates included in the models are described in Table 1.5.

Model	R^2	**K**	**AIC**	**AICc**	**ΔAICc**	**Akaike Weight**
TT + AD + TT*AD	0.20	5	333.73	334.50	0.00	0.50
TT + RC + AD + TT*AD†	0.23	7	334.87	336.34	1.84	0.20
TT + AD	0.14	4	337.51	338.02	3.52	0.09
TT + FP + AD + FP*AD	0.17	6	338.89	339.98	5.48	0.03
TT + FP + TT*FP	0.14	5	339.68	340.45	5.95	0.03
TT	0.10	3	340.17	340.47	5.97	0.03
TT + FP	0.12	4	340.24	340.75	6.25	0.02
TT + UD	0.11	4	340.84	341.34	6.84	0.02
TT + RC + MY + RC*MY	0.20	8	339.77	341.69	7.19	0.01
TT + YC	0.11	4	341.24	341.75	7.25	0.01
TT + RC	0.13	5	341.15	341.92	7.42	0.01
TT + MY	0.10	4	342.14	342.64	8.14	0.01
TT + EM	0.10	4	342.15	342.65	8.15	0.01
TT + SC	0.10	4	342.17	342.68	8.18	0.01
TT + RC + RC*TT	0.17	7	341.22	342.70	8.20	0.01
TT + PC	0.11	5	343.24	344.01	9.51	0.00
TT + RC + AD + RC*AD	0.18	8	342.21	344.13	9.63	0.00
TT + RC + MY + AD + RC*MY + RC*MY*AD	0.26	12	341.67	346.06	11.56	0.00

Table continued…

Table continued…

Intercept Only	0.00	2	346.63	346.78	12.28	0.00
TT + RC + FP + RC*FP	0.15	8	344.89	346.81	12.31	0.00
TT + RC + FP + MY + AD + RC*MY + RC*MY*AD	0.26	13	342.81	348.01	13.51	0.00

† *a posteriori* model

Table 2.13. Ranking of *a priori* models used to analyze the effect of duration of occupancy on total number of female attacks by Barred and Northern Spotted Owls for 80 experimental playback trials conducted in northwestern California. AICc is a small sample size correction factor for AIC. ΔAICc is the difference in AICc units between a given model and the top-ranking model. Akaike weight is the probability that a given model is the best-approximating model of the models tested. Covariates included in the models are described in Table 1.5.

Model	R^2	**K**	**AIC**	**AICc**	**ΔAICc**	**Akaike Weight**
Intercept Only	0.00	2	232.50	232.66	0.00	0.19
TT + AD + TT*AD	0.07	5	232.49	233.30	0.64	0.14
TT + AD	0.05	4	232.81	233.34	0.68	0.14
TT	0.01	3	233.73	234.04	1.38	0.10
TT + RC + FY + AD + RC*FY + RC*FY*AD	0.25	12	229.39	234.05	1.39	0.10
TT + RC + AD + RC*AD	0.14	8	232.02	234.05	1.39	0.10
TT + YC	0.02	4	234.92	235.45	2.79	0.05
TT + SC	0.01	4	235.30	235.83	3.17	0.04
TT + FY	0.01	4	235.30	235.84	3.18	0.04
TT + EM	0.01	4	235.65	236.19	3.53	0.03
TT + RC	0.04	5	235.43	236.24	3.58	0.03
TT + UD	0.01	4	235.73	236.26	3.60	0.03
TT + RC + RC*TT	0.07	7	236.71	238.27	5.61	0.01
TT + PC	0.01	5	237.67	238.49	5.83	0.01
TT + RC + FY + RC*FY	0.05	8	240.04	242.07	9.41	0.00

Table 2.14. Ranking of *a priori* and *a posteriori* models used to analyze male strike latency by Barred and Northern Spotted Owls for 126 experimental playback trials conducted in northwestern California. AICc is a small sample size correction factor for AIC. ΔAICc is the difference in AICc units between a given model and the top-ranking model. Akaike weight is the probability that a given model is the best-approximating model of the models tested. Covariates included in the models are described in Table 1.5.

Model	R^2	**K**	**AIC**	**AICc**	**ΔAICc**	**Akaike Weight**
TT + TC + AD	0.54	5	949.86	950.36	0.00	0.13
TT + TC	0.53	4	950.09	950.42	0.06	0.13
TT + TC + FP	0.54	5	950.31	950.81	0.45	0.11
TT + TC + FP + AD†	0.54	6	950.43	951.14	0.78	0.09
TT + TC + FP + TT*FP	0.55	7	950.45	951.40	1.04	0.08
TT + TC + EM	0.53	5	951.48	951.98	1.62	0.06
TT + TC + UD	0.53	5	951.54	952.04	1.68	0.06
TT + TC + PC	0.54	6	951.68	952.39	2.03	0.05
TT + TC + SC	0.53	5	951.97	952.47	2.11	0.05
TT + TC + AD + TT*AD	0.55	7	951.55	952.49	2.13	0.05
TT + TC + FP + AD + FP*AD	0.55	7	951.58	952.53	2.17	0.04
TT + TC + YC	0.53	5	952.09	952.59	2.23	0.04
TT + TC + RC	0.54	6	951.90	952.61	2.25	0.04
TT + TC + RC + FP + RC*FP	0.56	9	952.09	953.65	3.28	0.03
TT + TC + FP + AD + TT*FP†	0.56	9	952.19	953.74	3.38	0.02
TT + TC + RC + AD + RC*AD	0.56	9	952.50	954.05	3.69	0.02
TT + TC + RC + RC*TT	0.55	10	956.43	958.34	7.98	0.00
Intercept Only	0.00	2	1041.20	1041.30	90.94	0.00

† *a posteriori* model

Table 2.15. Ranking of *a priori* and *a posteriori* models used to analyze male and female strike latency by Barred and Northern Spotted Owls for 126 experimental playback trials conducted in northwestern California. AICc is a small sample size correction factor for AIC. ΔAICc is the difference in AICc units between a given model and the top-ranking model. Akaike weight is the probability that a given model is the best-approximating model of the models tested. Covariates included in the models are described in Table 1.5.

Model	R^2	**K**	**AIC**	**AICc**	**ΔAICc**	**Akaike Weight**
TT + TC + RC + AD + RC*AD	0.55	10	957.86	959.77	0.00	0.27
TT + TC + AD	0.52	6	959.35	960.06	0.29	0.23
TT + TC + RC + AD†	0.53	8	960.04	961.27	1.50	0.13
TT + TC	0.50	5	961.43	961.93	2.16	0.09
TT + TC + RC	0.52	7	961.83	962.78	3.00	0.06
TT + TC + UD	0.50	6	963.08	963.79	4.02	0.04
TT + TC + EM	0.50	6	963.10	963.81	4.04	0.04
TT + TC + SC	0.50	6	963.17	963.88	4.11	0.03
TT + TC + AD + TT*AD	0.52	8	962.76	963.99	4.22	0.03
TT + TC + PC	0.51	7	963.11	964.06	4.29	0.03
TT + TC + YC	0.50	6	963.40	964.10	4.33	0.03
TT + TC + RC + AD + TT*AD†	0.53	10	963.56	965.48	5.71	0.02
TT + TC + RC + RC*TT	0.52	11	967.88	970.20	10.43	0.00
Intercept Only	0.00	2	1171.01	1171.11	211.34	0.00

† *a posteriori* model

Table 2.16. Ranking of *a priori* and *a posteriori* models used to analyze male strike latency by Barred and Northern Spotted Owls, conditional upon a male response, for 79 experimental playback trials conducted in northwestern California. AICc is a small sample size correction factor for AIC. ΔAICc is the difference in AICc units between a given model and the top-ranking model. Akaike weight is the probability that a given model is the best-approximating model of the models tested. Covariates included in the models are described in Table 1.5.

Model	R^2	**K**	**AIC**	**AICc**	**ΔAICc**	**Akaike Weight**
TT + TC + AD	0.44	6	627.52	627.78	0.00	0.16
TT + TC + AD + TT*AD	0.47	8	627.61	627.97	0.18	0.15
TT + TC + PC + AD + PC*AD†	0.50	10	627.68	628.13	0.35	0.14
TT + TC + PC + AD†	0.47	8	627.83	628.18	0.40	0.13
TT + TC + PC + AD + TT*AD†	0.49	10	627.81	628.27	0.49	0.13
TT + TC + PC	0.44	7	629.76	630.07	2.29	0.05
TT + TC	0.41	5	630.06	630.28	2.50	0.05
TT + TC + RC	0.43	7	631.00	631.31	3.53	0.03
TT + TC + EM	0.41	6	631.55	631.81	4.03	0.02
TT + TC + FP + AD + FP*AD	0.44	8	631.52	631.87	4.09	0.02
TT + TC + SC	0.41	6	631.61	631.88	4.10	0.02
TT + TC + RC + AD + RC*AD	0.47	10	631.50	631.95	4.17	0.02
TT + TC + UD	0.41	6	631.76	632.02	4.24	0.02
TT + TC + FP	0.41	6	631.85	632.11	4.33	0.02
TT + TC + YC	0.41	6	632.00	632.27	4.49	0.02
TT + TC + FP + TT*FP	0.42	8	634.46	634.82	7.03	0.00
TT + TC + RC + RC*TT	0.46	11	634.39	634.90	7.12	0.00
TT + TC + RC + FP + RC*FP	0.44	10	635.17	635.63	7.85	0.00
Intercept Only	0	2	665.67	665.76	37.98	0.00

† *a posteriori* model

Table 2.17. Ranking of *a priori* models used to analyze male and female strike latency by Barred and Northern Spotted Owls, conditional upon a male and/or female response, for 86 experimental playback trials conducted in northwestern California. AICc is a small sample size correction factor for AIC. ΔAICc is the difference in AICc units between a given model and the top-ranking model. Akaike weight is the probability that a given model is the best-approximating model of the models tested. Covariates included in the models are described in Table 1.5.

Model	R^2	**K**	**AIC**	**AICc**	**ΔAICc**	**Akaike Weight**
TT + TC + AD	0.46	6	680.18	681.24	0.00	0.54
TT + TC + RC + AD + RC*AD	0.50	10	680.92	683.86	2.61	0.15
TT + TC + AD + TT*AD	0.47	8	682.85	684.72	3.48	0.10
TT + TC	0.41	5	685.29	686.04	4.80	0.05
TT + TC + PC	0.44	7	684.74	686.17	4.93	0.05
TT + TC + RC	0.44	7	684.79	686.23	4.99	0.04
TT + TC + SC	0.42	6	686.67	687.73	6.49	0.02
TT + TC + EM	0.42	6	687.01	688.07	6.83	0.02
TT + TC + UD	0.42	6	687.17	688.23	6.99	0.02
TT + TC + YC	0.42	6	687.20	688.27	7.02	0.02
TT + TC + RC + RC*TT	0.47	11	689.23	692.80	11.55	0.00
Intercept Only	0.00	2	725.36	725.51	44.26	0.00

Table 2.18. Values of HIC_{15}, which measures the potential for injury due to blunt force, for Barred and Northern Spotted Owl strikes directed at the head of the taxidermy mount during playback trials.

Replicate	**HIC_{15} for Barred Owl Strikes**	**HIC_{15} for Northern Spotted Owl Strikes**
1	61.82	62.28
2	64.12	33.29
3	35.80	132.25
4	77.02	60.49
5	58.12	59.49
6	83.33	98.91
7	38.49	54.34
8	40.65	125.77
9	-	127.74
10	-	26.92
11	-	318.24
12	-	212.81
13	-	132.35
14	-	145.69
Mean	57.42	113.61
Standard Error	5.90	20.19
95% Confidence Interval	45.86, 68.98	74.04, 153.18

Table 2.19. Comparison of HIC_{15} estimates resulting from pendulum strikes to the model owl head when the bob mass equaled 131.7 or 211.0 grams and the bob was raised to a height of 50.8cm.

Bob Mass (g)	**Bob Height (cm)**	**Replicate**	**HIC_{15}**	**Bob Mass (g)**	**Bob Height (cm)**	**Replicate**	**HIC_{15}**
131.7	50.8	1	26.36	211	50.8	1	45.08
131.7	50.8	2	30.49	211	50.8	2	32.66
131.7	50.8	3	13.60	211	50.8	3	16.99
131.7	50.8	4	8.42	211	50.8	4	20.25
131.7	50.8	5	6.91	211	50.8	5	38.19
131.7	50.8	6	14.13	211	50.8	6	12.96
131.7	50.8	7	6.55	211	50.8	7	27.11
131.7	50.8	8	27.04	211	50.8	8	22.42
131.7	50.8	9	25.39	211	50.8	9	30.25
131.7	50.8	10	7.92	211	50.8	10	27.98
Mean			**16.68**	**Mean**			**27.39**

Table 2.20. A comparison of HIC_{15} estimates resulting from pendulum strikes to model owl head when bob mass equaled 131.7 or 211.0 grams and bob was raised to a height of 115.06cm.

Bob Mass (g)	**Bob Height (cm)**	**Replicate**	***HIC***	**Bob Mass (g)**	**Bob Height (cm)**	**Replicate**	***HIC***
131.7	115.06	1	112.66	211	115.06	1	84.50
131.7	115.06	2	38.58	211	115.06	2	66.17
131.7	115.06	3	113.85	211	115.06	3	73.84
131.7	115.06	4	67.23	211	115.06	4	149.40
131.7	115.06	5	102.09	211	115.06	5	123.55
131.7	115.06	6	45.27	211	115.06	6	143.17
131.7	115.06	7	179.46	211	115.06	7	89.41
131.7	115.06	8	80.38	211	115.06	8	78.75
131.7	115.06	9	52.13	211	115.06	9	85.05
131.7	115.06	10	43.09	211	115.06	10	88.37
Mean			**83.47**	**Mean**			**98.22**

Table 2.21. Relative support for the "exclusion" and "acquiescence" hypotheses based on model-averaged treatment type (*TT*) effect on attack code, total number of attacks, and strike latency for the all inclusive and conditional analyses. (+) indicates weak support for the hypothesis (i.e., 95% CI for (*TT*) barely overlapped zero), (+ +) indicates strong support for the hypothesis (i.e., the 95% confidence interval for (*TT*) did not overlap zero), (0) indicates no substantial difference among treatments (i.e., 95% CI strongly overlapped 0), (−) indicates weak evidence against the hypothesis (i.e., 95% CI for (*TT*) barely overlapped zero), and (− −) indicates strong evidence against the hypothesis (i.e., 95% CI for (*TT*) did not overlap zero).

	All Trials		**Trials with a response only**	
Response Variable	Exclusion Hypothesis BAOW/SPOW† Treatment	Acquiescence Hypothesis SPOW/BAOW† Treatment	Exclusion Hypothesis BAOW/SPOW† Treatment	Acquiescence Hypothesis SPOW/BAOW† Treatment
Attack Code				
Male	+	+ +	+ +	+ +
Territory	0	+	+	+
Total Number of Attacks				
Male	−	+	−	+
Territory	−	+	−	0
Strike Latency				
Male	0	0	0	0
Territory	0	0	0	0

† For each treatment type the first acronym represents the resident species followed by the playback species that was presented to the resident species.

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APPENDIX I

Elastic Collision Application for Owl Strikes

I investigated the acceleration of a taxidermy owl mount's head following a collision with an attacking owl, and how it relates to that of an elastic collision. Although collisions of bodies occurring in nature are typically not perfectly elastic, collisions between two rigid bodies are frequently approximated as such (Halliday et al. 2001). In elastic collisions, momentum and kinetic energy are conserved within the system with no kinetic energy being lost in the deformation of either body. The exclusion hypothesis predicts that heavier Barred Owls have the ability to deliver strikes with an increased capacity to cause injury compared to Northern Spotted Owls. To determine whether physics theory supported the exclusion hypothesis, I applied a range of owl masses and flight velocities to the elastic collision equation:

$$v2_f = \left[\frac{2 * m2}{2 * m2}\right] * v1_i$$

Where: $v1_i$ = attacker velocity before contact with the mount's head

$v2_{f=}$ velocity of mount's head after contact with the attacking owl

m1 = attacking owl's body mass

m2 = mass of taxidermy mount's head (61g)

I calculated final head velocities using an average body mass for a male Northern Spotted Owl (combination of species and gender with the lowest average body mass) of 579g and female Barred Owl (combination of species and gender with greatest average body mass) of 873g (Mazur and James 2000). Because flight velocities for Barred and Northern Spotted Owls are unknown, I used attacking owl velocities of 30 and 45 mph (or 13.41 and 20.12 m/s respectively) in the calculations (Table 2.22).

Table 2.22. Resultant velocity of owl model's head based on elastic collision calculations with varying attacker body mass and flight velocity.

Attacker Body Mass (g)	Attacker Flight Velocity (m/s)	Resultant Velocity of Model's Head (m/s)
579 (Male Northern Spotted Owl)	13.41	24.26
579 (Male Northern Spotted Owl)	20.12	36.4
873 (Female Barred Owl)	13.41	25.07
873 (Female Barred Owl)	20.12	37.61

The results of the elastic collision calculations demonstrated that a 50.7% increase in attacker body mass (579g to 873g) produced a 3.3% increase in resultant head velocity following a collision when the attacker's initial velocity was 13.41 or 20.12 m/s. In comparison, a 50% increase in attacker flight velocity prior to a strike (from 13.41 to 20.12 m/s) produced a 50% increase in the resultant velocity experienced by the head of the owl mount at either attacker body mass. Therefore, attacker flight velocity appears to have a much greater influence over the HIC_{15} value delivered by an attacker compared to body mass for the velocities and masses investigated.