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Who hits and hoots at whom? Potential for interference competition between barred and northern spotted owls

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ABSTRACT

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 compete with northern spotted owls and may be one cause for recent declines in some northern spotted owl populations. Our focus was to examine whether barred owls have the potential to competitively exclude northern spotted owls from their territories through interference competition. We used a playback experiment to quantify aggressive vocal and physical behavior of barred and northern spotted owls during territorial defense. Experimental trials consisted of displaying northern spotted or barred owl taxidermy mounts, and broadcasting recorded vocalizations of the corresponding species, in both barred and northern spotted owl territories. The frequency of interspecific interactions was lower compared to intraspecific interactions between northern spotted owls alone. However, barred owls responded with higher levels of vocal and physical aggression than did northern spotted owls when agonistic interspecific interactions occurred. Our results suggest that barred owls are likely to assume the dominant role during interspecific interactions with northern spotted owls. Thus, interference competition is a plausible mechanism by which barred owls could contribute to observed population declines of northern spotted owls in areas where the species co-occur.

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1. Introduction

Mitigating threats to populations of northern spotted owls (*Strix occidentalis caurina*) has been the focus of intense study over the last 40 years. Observed population declines likely resulting from habitat loss led to the official listing of the northern spotted owl as a threatened species in 1990 (US Fish and Wildlife Service, 1990) and subsequent conservation efforts focused 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 (Anthony et al., 2006; USDA Forest Service and BLM, 1994). Competition between northern spotted

and barred owls (*Strix varia*) has been identified as another important potential threat to northern spotted owl populations (Anthony et al., 2006; Buchanan et al., 2007; Gutiérrez et al., 2007; Hamer et al., 1994; Kelly et al., 2003; Taylor and Forsman, 1976).

Historically, the distribution of barred owls was restricted to the eastern portion of the United States. However, the species' range has expanded westward over the past 50 years and now completely overlaps that of the northern spotted owl (Dark et al., 1998; Kelly et al., 2003; Livezey, 2009). Rapidly increasing barred owl populations in the western US, coupled with continued northern spotted owl population declines, suggests that competition with barred owls may threaten remaining northern spotted owl populations. Over the past decade, studies investigating the potential impact of barred owls on northern spotted owl populations found that colonization and extinction rates, territory occupancy, and survival of northern spotted owls may be negatively affected by the presence of barred owls (Anthony et al., 2006; Kelly et al., 2003; Olson et al., 2005).

Interspecific interference competition during territorial interactions could explain the witnessed impacts on northern spotted owls

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because of observed interactions between the two species (Dunbar et al., 1991; Herter and Hicks, 2000), some of which may represent intraguild predation (Leskiw and Gutiérrez, 1998). 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 reducing resource competition, reducing risk to offspring, and/or obtaining energetic benefits by consuming competitors (Sergio and Hiraldo, 2008). Several studies demonstrated intraguild predation in raptor communities that include owls (Martínez et al., 2008; Sergio et al., 2003, 2007; Zuberogoitia et al., 2008), supporting the idea that intraguild predation may exist in the northern spotted owl/barred owl system. In the presence of intraguild predation (Polis et al., 1989), the barred owl should fill the role of dominant competitor and predator during interactions with northern spotted owls because barred owls have larger body mass (\bar{x} = 630 and 800 g for males and females, respectively; Mazur and James, 2000) than northern spotted owls (\bar{x} = 600 and 654 g; Gutiérrez et al., 1995).

To determine whether interference competition is a plausible mechanism by which barred owls can contribute to northern spotted owl population declines, we conducted a series of playback experiments to quantify territorial encounters between the two species. By simulating inter- and intraspecific encounters and quantifying attack responses by territory residents, we addressed whether or not interference competition by barred owls could be a contributing factor to continued northern spotted owl population declines. Specifically, we investigated the Exclusion and Acquiescence Hypotheses where (1) the Exclusion Hypothesis predicts that barred owls actively exclude northern spotted owls through interference competition expressed as frequent vocal aggression and physical attacks with increased capacity to cause injury and (2) the Acquiescence Hypothesis predicts that northern spotted owls defend their territories with less vigorous calling and a reduced number of physical attacks against barred owls than against northern spotted owls.

2. Methods

We conducted experiments on four study areas which were concurrently surveyed for northern spotted and barred owls: Redwood National Park (RNP), Green Diamond Resource Company lands (GDRC), Hoopa Tribal lands (HOOPA), and the Willow Creek study area (WCSA, part of the Northwest California demographic study) in Humboldt and Trinity counties in northwestern California (see Anthony et al., 2006). RNP and the majority of GDRC lands are located within 32 km of the Pacific coast where redwood (*Sequoia sempervirens*) trees dominate forest over-stories and hardwood understories are predominated by tanoak (*Lithocarpus densiflorus*), red alder (*Alnus rubra*), and Pacific madrone (*Arbutus menziesii*) (Diller and Thome, 1999). Due to the proximity of 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 approximately 50 km east of RNP and the GDRC lands. The coniferous forests in these two study areas lack redwood trees and the over-stories of these two areas are dominated by Douglas fir (*Pseudotsuga menziesii*) mixed with hardwood species (Ting, 1998; Franklin et al., 2000). In general, the RNP and HOOPA sites appeared to have a greater proportion of historic northern spotted owl territories occupied by barred owls than do the WCSA and GDRC sites (Anthony et al., 2006). 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).

2.1. Experimental design

Using a quasi-experimental design, playback trials were conducted on barred and northern spotted owl territories from mid-May through mid-August in 2008 and 2009. Territories were considered the sampling unit and defined as 710 m radius circles (Franklin et al., 2000) centered on areas where owls had been detected during the current and preceding breeding seasons or areas where owls were determined to be actively breeding during the current field season. This collection of northern spotted and barred owl territories represented two separate sampling frames from which 63 territories for experimentation were randomly drawn each year, without replacement.

Playback trials for each territory were conducted within 100 m of the most recent daytime detection of territorial males within the current breeding season. If no daytime location was available, trials were conducted within 100 m of the most recent nighttime detection. We attempted to conduct playback trials on ridges to maximize resident owls detecting the playback and observers detecting vocalizations by the resident owls. Trials were conducted under three treatments consisting of the resident species occupying the territory (barred or northern spotted owl) and a single playback species presented within the resident territory (barred or northern spotted owl). For trials under the first treatment, a northern spotted owl taxidermy mount was presented and vocalizations broadcast in a northern spotted owl territory. This treatment was a local control to provide baseline data on intraspecific competition occurring among northern spotted owls. For trials in the second treatment a barred owl mount and vocalizations were presented in a northern spotted owl territory, and in the third treatment, a northern spotted owl mount and vocalizations were presented in a barred owl territory. To control for seasonal effects on territoriality (Reid et al., 1999; Waldo, 2002), trials for all treatments were assigned evenly across three seasonal periods (20 May–20 June, 21 June–20 July, 21 July–20 August) which corresponded to periods when owls were nesting, fledging young, and when fledged young were becoming independent (Franklin et al., 2000). Due to logistic constraints, actual sampling of treatment groups differed slightly from the targeted sample of seven trials/treatment/seasonal period (Van Lanen, 2010).

2.2. Playback procedures

All trials began 30–60 min after official sunset time (NOAA Earth System Research Laboratory, 2008) because northern spotted and barred owls are most active shortly after sunset but are still near their roost sites (Forsman et al., 1984; Odom and Mennill, 2010). We used taxidermy mounts made from salvaged northern spotted and barred owl carcasses. For each trial, the base of the appropriate taxidermy mount was affixed atop a 1.5 m tall aluminum pole along with an amplifying speaker oriented to broadcast sound in the direction the mount was facing. Together, the mount and speaker on the pole were, rotated 90° at 5 min intervals following the start of the playback to broadcast in all directions. Recorded vocalizations were played using a continuous compact disk (CD) recording lasting 60 min, with five periods of intermittent calling separated by approximately 4-min periods of silence. The composition of call types changed throughout the duration of the playback CD from territorial calls to aggressive territorial calls 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). In the event of a response, the time, species, and sex were documented, and resident vocalizations were recorded with an omni-directional microphone. Vocalizations of both northern spotted and barred owls were tabulated and

classified as either contact, territorial, or aggressive calls (Forsman et al., 1984; McGarigal and Fraser, 1985). The sex of the responding owl was determined by the tone and pitch of the vocal response (Franklin et al., 1996; Odom and Mennill, 2010) in the field and from audio recordings. Intermediate vocalizations that could not be confidently assigned to a particular sex were attributed to an individual of an unknown sex and were excluded from the analyses. Observers used night vision goggles to detect owls that silently approached the model. Some playback trials were truncated ($n = 9$, 7% of trials) because either (1) the responding individuals struck the owl mount and dislodged the head such that it could not be re-attached; the trial was truncated at the time of the strike or (2) neighboring hetero- or conspecifics responded during trials, which were truncated when the neighbor first vocalized because resident responses could no longer be attributed strictly to the playback treatment.

Instances where direct physical contact between a resident owl and the taxidermy mount or when a resident owl flew within 1 m of the mount with its legs lowered but no physical contact occurred were classified as “attacks.” Camcorders equipped with infrared lights were used to record footage of physical responses to the mount and this footage was later reviewed to confirm the nature and timing of attacks. To quantify the risk of head injury due to the blunt force of strikes, accelerations experienced by the head of the owl mount as a result of strikes by resident owls were recorded with a tri-axial analog accelerometer (PCB Piezotronics Model 356M162) that was placed in the head of the taxidermy mounts. A laptop computer powered the accelerometer through a signal conditioner (National Instruments NI USB-9162 with NI 9233 4 Channel Analogue Input). Acceleration data were recorded using LabView 8.5 Software (National Instruments Corporation) at a rate of 10,000 samples per second when “triggered” by a strike.

2.3. Data analyses

Competing biological hypotheses developed a priori were expressed as statistical models where the response variables were detection of any response, aggressive call frequency during responses, whether an attack occurred during a response, and total number of attacks during trials with a response (Table 1). Response variables were tabulated for the male resident only. Binary response variables (detection of a response and whether an attack occurred) were analyzed using logistic regression and continuous response variables were analyzed using generalized linear models

(PROC LOGISTIC and PROC GENMOD, respectively) implemented in SAS 9.1 (SAS Institute, 2003).

Analyses on the frequency of male resident responses to the treatment were conducted on the full set of 126 playback trials. To investigate the magnitude of male residents' responses when agonistic interactions occurred, we used a subset of 79 trials in which a male resident response was detected. Analyses with this subset of data were considered particularly important because trials where no resident response was observed could have resulted from residents not detecting the treatment, observers not detecting a resident response, or the residents not responding. An information-theoretic approach was used for all analyses (Burnham and Anderson, 2002) to select appropriate models for inference. Models resulting in quasi-complete separation in the logistic regression analyses (SAS Institute, 2003) were removed from the model set due to poor model convergence. Models were ranked in each model set using Akaike's Information Criterion for small sample sizes (AICc). Akaike weights were calculated for each model as the probability that a given model in the candidate model set was the best model for inference, given the data and the model set.

A priori models in each model set included the treatment effect (TT) as well as additive effects of covariates (Table 1) and two- and three-way interactions, which were thought to be biologically meaningful. Covariates such as study area and timing within the season (Ganey, 1990; Mazur and James, 2000; Waldo, 2002), lunar cycles (Ganey, 1990), breeding status of the resident pair (determined using methods described by Franklin et al. (1996)), and the duration of occupancy of territories by individuals (Hyman et al., 2004; Sergio et al., 2009) were considered important because of their potential effects on the rate and intensity of owl responses and were included to reduce potential confounding of treatment with other effects. Although the age of individuals may influence territorial aggressiveness, we were unable to include this as a covariate because the ages of individual barred owls were largely unknown throughout the study area. R^2 and maximum re-scaled R^2 values were used as measures of the proportion of variance explained by the models for continuous and binary response variables, respectively. For some model sets, additional models were constructed a posteriori, where combinations of additive effects and two-way interactions resulted in low Δ AICc values during the a priori analyses.

Effects were estimated for treatments where barred owl residents were presented with the northern spotted owl playback and where northern spotted owl residents were presented with

Table 1
Description of response variables and covariates used in analyses of data from experimental playback trials on barred and northern spotted owls conducted in northwestern California.

Variable	Acronym	Type	Description
<i>Response variables</i>			
Male response	–	Binary	Whether a male responded (1) or did not respond (0) during a trial
Male attacks	–	Binary	Whether a male attacked (1) or did not attack (0) the presented mount during the trial
Male aggressive call frequency	–	Continuous	Number of male aggressive calls per minute
Total number of male attacks	–	Continuous	Total number of male strikes and swoops during the trial
<i>Covariates</i>			
Treatment type	TT	Categorical	Combination of resident and playback species for each trial
Duration of territory occupancy	TY	Continuous	Known number of years male resident owl was observed on territory
Study area	SC	Categorical	Interior versus coastal study areas
Adjusted Julian date	AD	Continuous	Number of days after May 20 (the date of first trials)
Moon phase	MP	Continuous	Visible quarters of the moon at the end of the trial (1 = 1/4 moon, 2 = 1/2 moon, 3 = 3/4 moon, 4 = full moon)
Truncation code	TC	Categorical	Whether or not the trial was truncated for any reason
Year code	YC	Categorical	2008 versus 2009 field seasons
UTM days	UD	Continuous	Number of days between the last known owl location and the playback trial
Reproductive code	RC	Categorical	Whether residents were reproductively active, inactive, or of undetermined status
Pair code	PC	Categorical	Whether residents were single, paired, or of undetermined pair status
Female presence	FP	Categorical	Whether or not the resident female was detected during the trial

the barred owl playback by setting the intercept as the treatment where northern spotted owl residents received the northern spotted owl treatment. Predictions of the Exclusion Hypothesis were assessed 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. To account for model selection uncertainty, we model-averaged across all models in a given model set except the intercept-only model. Using these model-averaged values, we provide unconditional estimates of parameters ($\hat{\beta}$) and 95% confidence intervals (Burnham and Anderson, 2002).

Using data from the accelerometer, 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 (Beckwith et al., 2007; Pfister et al., 2009; Turchi et al., 2004). HIC was calculated over a period of 15 ms (HIC_{15}) (Jackson et al., 2002; Pfister et al., 2009) for all strikes to account for the entire acceleration event recorded by the accelerometer. An HIC_{15} value for each strike 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 $(t_2 - t_1) = 0.015$ s and $a(t)$ = the magnitude of the resultant three-dimensional acceleration in g's occurring at time (t).

3. Results

3.1. Vocal responses

We recorded 79 male responses ($n = 18$ barred owl responses during 39 trials, $n = 61$ northern spotted owl responses during 87 trials) during the 126 playback trials conducted. In the analysis examining whether a response was detected or not, the top-ranked logistic regression model was almost six times more likely than the second-ranked model, and accounted for 28% of the variation in the data (Table 2). Together, the top two models accounted for all of

the Akaike weight, with these two models differing only by inclusion of an interaction in the second-ranked model (Table 2). Both models included whether a female was present during the trial (FP), which was positively associated with male responses ($\hat{\beta} = 1.02$, 95% CI = 0.52, 1.51). Based on the 95% confidence intervals, model-averaged estimates of TT indicated male barred owl residents responded similarly to the northern spotted owl treatment as male northern spotted owls did to the barred owl treatment (Table 3).

When males responded ($n = 79$ trials), the top-ranked generalized linear model for male calling frequency was an a posteriori model, which included adjusted Julian date (AD), female presence (FP) and the interaction of TT with AD (Table 2). This model explained 38% of the variation in the data (Table 2). The AD covariate was incorporated in each of the top seven models (combined Akaike weight = 0.99) and appeared to negatively influence call frequency ($\hat{\beta} = -0.02$, 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 ($\hat{\beta} = 0.55$, 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 (Table 3). In contrast, male northern spotted owls called less frequently in response to the barred owl treatment than toward the northern spotted owl treatment (Table 3).

3.2. Physical attacks

In the analysis of whether males attacked during responses ($n = 79$ trials), TT and adjusted Julian date (AD) were present in the top two logistic regression models, which had a combined Akaike weight = 0.60 (Table 2) and explained 35% and 36% of the variation in the data, respectively. Model-averaged estimates of the effect size of AD suggested that male residents were less likely to attack as the season progressed ($\hat{\beta} = -0.03$, 95% CI = -0.06 , 0.01). Barred owls were more likely to attack the northern spotted owl model and northern spotted owls were less likely to attack the barred owl model than northern spotted owls receiving the northern spotted owl treatment (Table 3).

Table 2

Ranking of a priori and a posteriori models from four analyses of male barred and northern spotted owl responses to experimental playback trials conducted in northwestern California. Covariates included in the models are described in Table 1. Only models with Akaike weights ≥ 0.05 are shown for each analysis.

Model	R^2	K	$\Delta AICc^a$	Akaike weight ^b
General response ($n = 126$ trials)				
$TT + FP$	0.28	4	0.00	0.85
$TT + FP + TT*FP$	0.28	6	3.53	0.15
Male aggressive call frequency – responses only ($n = 79$)				
$TT + FP + AD + TT*AD^c$	0.38	8	0.00	0.73
$TT + AD + TT*AD$	0.33	7	3.58	0.12
$TT + FP + AD + FP*AD$	0.32	7	5.19	0.05
$TT + RC + FP + AD + RC*AD^c$	0.38	10	5.59	0.05
If male attacked – responses only ($n = 79$)				
$TT + AD$	0.35	4	0.00	0.51
$TT + AD + TT*AD$	0.36	6	3.35	0.09
$TT + TC$	0.29	4	3.37	0.09
$TT + RC$	0.32	5	4.30	0.06
$TT + FP + AD + FP*AD$	0.35	6	4.60	0.05
TT	0.24	3	4.82	0.05
Total number of male attacks – responses only ($n = 79$)				
$TT + AD + TT*AD$	0.25	7	0.00	0.65
$TT + AD$	0.18	5	2.10	0.23
$TT + FP + AD + FP*AD$	0.20	7	4.87	0.06

^a Difference in AICc units between a given model and the top-ranking model.

^b Probability that a given model is the best-approximating model of the models in the set.

^c A posteriori model.

Table 3

Model-averaged estimates and 95% confidence intervals for treatment effects of male barred owl residents presented with northern spotted owl treatment (BAOW/SPOW) and male northern 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.

Analysis	BAOW/SPOW treatment		SPOW/BAOW treatment	
	Estimate	95% CI	Estimate	95% CI
<i>All trials (n = 126)</i>				
Whether response detected	−0.47	−1.09, 0.16	−0.11	−0.69, 0.48
<i>Response trials (n = 79)</i>				
Calling frequency	1.04	0.01, 2.08	−1.22	−2.33, −0.11
Whether attack occurred	1.42	0.25, 2.59	−2.02	−3.73, −0.31
Total number of attacks	−1.00	−3.13, 1.13	−2.65	−5.84, 0.54

Given that a male response was detected, the three top-ranked generalized linear models predicting the total number of male attacks per trial ($n = 79$ trials) included the *AD* variable, which indicated that the number of attacks decreased as the summer progressed ($\hat{\beta} = -0.03$, 95% CI = -0.08 , 0.01 ; cumulative Akaike weight of 0.94; [Tables 2 and 3](#)). Model-averaged parameter estimates for *TT* suggested that there was no difference between barred and northern spotted owls residents receiving the interspecific playback treatments relative to northern spotted owl residents responding to the northern spotted owl treatment ([Table 3](#)).

Accelerometer data were collected from eight strikes directed at the northern spotted owl taxidermy mount by five male barred owls and 14 strikes directed at the northern spotted owl mount by two male northern spotted owls. Based on these data, 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, indicating that northern spotted owls struck the taxidermy mounts with an increased capacity to cause head injury compared to barred owls.

4. Discussion

We observed both intra- and interspecific responses by male resident northern spotted and barred owls. Interspecific interactions occurred less frequently than did intraspecific interactions between northern spotted owls alone. However, when interspecific interactions occurred, barred owls had a higher calling frequency and a larger number of trials resulting in a strike relative to northern spotted owls, indicating that barred owls likely would act as the dominant species during agonistic encounters with northern spotted owls.

4.1. Acquiescence versus exclusion hypotheses

In general, the Acquiescence Hypothesis was largely supported because northern spotted owls called less often, attacked less frequently, and attacked fewer times overall when presented with the barred owl treatment than when they received the northern

spotted owl treatment ([Table 4](#)). However, similar response frequencies between treatments and an increased capacity for northern spotted owl strikes to cause head injury did not meet predictions of the Acquiescence Hypothesis. The Acquiescence Hypothesis has also been partially supported by previous studies where northern spotted owls responded less often to broadcast calls from conspecifics after barred owl calls were broadcast in an area ([Crozier et al., 2006](#)) and northern spotted owls had lower detection probabilities in the presence of barred owls ([Bailey et al., 2009](#); [Olson et al., 2005](#)). [Crozier et al. \(2006\)](#) also found that northern spotted owls responded less often in areas with higher barred owl density, suggesting that northern spotted owls may exhibit shifts in vocal behavior in the presence of barred owls.

We found mixed support for the Exclusion Hypothesis ([Table 4](#)). Barred owls gave more aggressive calls and struck the northern spotted owl model more frequently than northern spotted owls did, both of which agreed with the Exclusion Hypothesis. However, male barred owls responded less frequently and their strikes exhibited a reduced capacity to cause injury from blunt force, which contradicted our predictions. Despite general support for the prediction that intraspecific competition is generally stronger than interspecific competition ([Connell, 1983](#)), the reduced frequency of responses by barred owls receiving the northern spotted owl treatment was 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](#)). Although [Wiens et al. \(2011\)](#) also found that barred owls responded less frequently to spotted owl calls than spotted owls, the lower response frequency by barred owls we observed may have been influenced by the fact that 84% of trials in northern spotted owl territories were set-up within 100 m of daytime locations while 66% of trials in barred owl territories were at daytime locations. This difference in trial locations between treatments could have negatively biased results because residents would likely respond to treatments when the trial site was closer to their territory center.

Dominance in interspecific interactions can be strongly influenced by body mass between competing owl species ([Martínez et al., 2008](#)), and the results of our study were in keeping with this expectation because male barred owls (the larger species) gave

Table 4

Relative support for the exclusion and acquiescence hypotheses based on model-averaged treatment type (*TT*) effects on whether responses occurred, aggressive calling frequency, whether an attack occurred, and the total number of attacks. (+) 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 largely overlapped 0), (−) indicates weak evidence against the hypothesis (i.e., 95% CI for (*TT*) barely overlapped zero).

Response variable	Exclusion hypothesis BAOW/SPOW ^a treatment	Acquiescence hypothesis SPOW/BAOW ^a treatment
Response	−	0
Aggressive call frequency	++	++
Attacks	++	++
Total number of attacks	−	+

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

aggressive calls more frequently and attacked northern spotted owl mounts in more trials than did the smaller northern spotted owls. Leskiw and Gutiérrez's (1998) suggestion that such attacks could result in northern spotted owl mortality may explain the observed reduction of northern spotted owl survival in the presence of barred owls (Anthony et al., 2006). Effects of even occasional intraguild predation can extend beyond the immediate individual effects to the population and community levels by reducing fitness due to predator avoidance, changing foraging behavior, and reducing the ability of individuals to find mates and to hold territories (Hakkarainen and Korpimäki, 1996; Lima and Dill, 1990; Sergio et al., 2007). Mikkola (1976) found that smaller owls were occasionally in diets of larger owls, but rarely the reverse. Furthermore, generalist owls engaged in intraguild predation far more frequently than did specialists, presumably because they could gain energetic benefits from the consumption of a competitor (Mikkola, 1976). Fewer physical responses to barred owls by northern spotted owls may ultimately be a result of greater trophic specialization by this species or may have evolved through reduction of interspecific physical altercations to avoid potential predation by larger owls.

Encounters between barred and northern spotted owls appear to have three potential outcomes with northern spotted owls (1) acquiescing and ultimately being displaced, (2) responding aggressively and maintaining possession of their territories, or (3) responding aggressively and being either injured or killed during the encounter. The interactions between barred and northern spotted owls observed in this study appear to demonstrate elements of both the Acquiescence and Exclusion Hypotheses and may ultimately depend on individual variation. However, the apparent reduction in northern spotted owl populations in some areas of co-occurrence (Anthony et al., 2006) suggests that barred owls are assuming the dominant role during interspecific interactions and may effectively outcompete their congeners in areas of sympatry.

4.2. Potential for injury from attacks

Northern spotted owls appear to have a greater potential to cause trauma from blunt force during strikes than do barred owls. Van Lanen (2010) used a pendulum experiment with representative masses for these two species to determine the relative effects of attacker mass and velocity on HIC_{15} values resulting from collisions. This work demonstrated that attacker flight velocity immediately prior to impact has a larger effect on the resultant head acceleration following a strike than attacker body mass. As a smaller and presumably more maneuverable species, northern spotted owls are likely able to reach greater flight velocities than barred owls in the confined understory of the forest types where trials took place. Our findings 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, if northern spotted and barred owls can tolerate different magnitudes of blunt force, or whether there is a threshold beyond which injuries will result regardless of the magnitude of blunt force.

Our measure of blunt force failed to account for potential injury due to punctures or lacerations inflicted by talons. Talon grip force of raptors increases exponentially with body mass (Ward et al., 2002); therefore, it is possible that injuries resulting from puncture wounds and lacerations may allow barred owls to inflict mortal wounds.

4.3. Competitive exclusion of northern spotted owls?

The intensity of vocal and physical interactions between barred and northern spotted owls estimated in this study suggests that

barred owls 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. As generalist predators, barred owls may exist at higher densities than northern spotted owls (Hamer et al., 2007), and may be superior at resource exploitation (Hamer et al., 2001), which could ultimately result in exclusion of northern spotted owls.

Although displacement of northern spotted owls by barred owls appears to be the most likely outcome, viable populations of northern spotted owls may persist under a number of scenarios. Responses to playbacks were highly variable and indicated a substantial degree of behavioral plasticity among individuals, which might result from heritable genetic differences. Future studies of this and other systems should attempt to identify and isolate whether behavioral plasticity results from genetic differences or is influenced by environmental factors (e.g., habitat and prey conditions) and individual characteristics (e.g., age, breeding status). 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 (Andrén, 1990; Fretwell and Lucas, 1970; Klomp, 1972). By preserving high-quality northern spotted owl habitat, these aggressive individuals may be at a selective advantage, assuming residents of these high-quality sites produce offspring that are subsequently recruited into the population. Changes in the frequency of heritable traits for aggression within northern spotted owl populations could result in a positive shift in the frequency that northern spotted owls retain their territories in the presence of barred owls.

Additionally, individual behavioral shifts 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 (Hamer et al., 2007; Herter and Hicks, 2000; Pearson and Livezey, 2003), making risk-sensitive habitat selection and spatial avoidance possible. Also, northern spotted owls may learn to exhibit short-term behavioral avoidance to reduce the frequency of agonistic interactions with barred owls. Some evidence suggests 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 (Crozier et al., 2006).

Interspecific interference competition is likely occurring in this system with barred owls assuming the role of dominants during interactions. This suggests that long-term persistence of viable northern spotted owl populations will likely depend upon a variety of factors including behavioral shifts by northern spotted owls to reduce competition in the presence of barred owls over time, plasticity in territorial aggression by northern spotted owls, the existence of refugia within the current northern spotted owl's range affording this species habitat-mediated or distance-sensitive avoidance of competitors, or the active management of barred owl populations to conserve northern spotted owls.

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