

SONG DISCRIMINATION OF NEIGHBORS AND STRANGERS BY
MALE TERRITORIAL NORTHERN SPOTTED OWLS
(*Strix occidentalis caurina*)

by

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ABSTRACT

Song Discrimination of Neighbors and Strangers by Male Territorial Northern Spotted Owls (*Strix occidentalis caurina*)

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Studies of song communication in passerine birds have supported the “dear enemy” hypothesis which states that neighboring territory owners should develop stable relationships over time to reduce energetically costly behavioral interactions. Songs and calls may provide details regarding kinship, territory boundaries, neighbor recognition, and even individual recognition. I tested the “dear enemy” hypothesis to examine the response of male Northern Spotted Owls (*Strix occidentalis caurina*) to call playbacks of their neighbors and strangers as well as to calls of their neighbors in a novel location (opposite territory boundary). A bird that can discriminate between neighbor’s songs and associate each with a particular location (hence the opposite boundary test) may demonstrate individual recognition. I conducted a field experiment to examine song discrimination by playing three different treatments to my subjects. Two call playback treatments (neighbor and stranger) and a control were played at the boundary that borders the territory of each tested individual and its neighbor, with a third treatment on the opposite boundary (opposite neighbor). I tested three response variables 1) latency to first response, 2) number of calls given

within the test period, and 3) average time between calls. I used a crossover experimental design where I blocked for possible sources of variation such as season and time of day. Of the three response variables, latency showed a significant treatment effect with owls responding sooner to strangers than to neighbors. This supported the “dear enemy” hypothesis. The opposite neighbor treatment produced unpredicted results from tested individuals in that their first response took the greatest amount of time. However, once they responded it was with the most intensity. The delayed reaction results may suggest a confusion effect or delayed recognition. Time of year and order of treatments also influenced the responses. Such sources of variation can play a large role in the outcomes of avian playback experiments and should be considered in future experimental designs for any playback studies.

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INTRODUCTION

A territory is a breeding area within which nesting, courtship, mating, and most food seeking usually occurs (Lack 1939). Behaviors characteristic of territoriality may include self-advertisement, defense of an area, and restriction of most behaviors to a limited and defined area (Hinde 1956). Two key purposes for holding and defending a territory are food resources and mating opportunities (Catchpole 1989). These two purposes are not necessarily mutually exclusive because food resources may aid mating opportunities. The benefits gained by expending energy to defend a territory must warrant that extra energy output. Benefits for birds include exclusive access to resources like food, nest sites, and mates. Costs of defending a territory may include increased risk of predation, injury, or time lost signaling and mate guarding (Bradbury and Vehrencamp 1998).

Northern Spotted Owls (*Strix occidentalis caurina*) are highly territorial (Forsman et al. 1984) and have relatively large home ranges (Gutiérrez et al. 1995). During the breeding season in northern California, home ranges span at least 190 to 680 hectares (Solis and Gutiérrez 1990). Home range sizes of Northern Spotted Owls vary with topography and season (Forsman et al. 1984), and can overlap in time and space (Forsman et al. 1984, Solis and Gutiérrez 1990). Territories are included within annual home ranges and are generally occupied continuously unless birds are displaced by habitat destruction (Forsman et al. 1984). Included within the general defended territory would be the core nesting area. Within their home ranges,

spotted owls not only sequester food and mates, but also find areas for nest sites, thermoregulation, and predator concealment (Gutiérrez and Carey 1985). Northern Spotted Owls are also long-lived, monogamous, show high site fidelity (Forsman et al. 1984), and high survival on established territories (Franklin et al. 2000). Similar to the behavior of many owls, the Northern Spotted Owl is nocturnal and vocalizations serve as their primary means of territorial defense (Forsman et al. 1984).

Thirteen call types have been documented for the Northern Spotted Owl (Forsman et al. 1984). Both sexes give most call types although, females are distinguished by higher pitched calls. Calls which are easily distinguishable and frequently given by both males and females include the four-note location call, series location call, crowbark, and contact call (Forsman et al. 1984). According to Forsman et al. (1984), the four-note location call functions as a general locator call between mated birds as well as for territory defense. During territorial disputes the four-note location call is used in combination with other calls. Use of vocalizations probably enables a bird to defend a larger area than could be defended using physical movements alone. For this to be true, songs used in territorial defense must have evolved under selection pressures that help maximize the distance songs travel (Klump 1996). Not only have bird songs evolved to travel over long distances but the structural morphology of their ears has evolved for receiving auditory signals (Wiley and Richards 1982). The ability of an auditory signal to travel, and the capability of using auditory cues to determine distance of the signaler, increases the efficiency of

defending a territory (Naguib 1995). Thus, vocalizing may be more effective in defending larger areas than could be done with actual physical movements alone (Naguib 1995).

Use of song is an extremely effective form of territory defense (Kroodsma 1977, Falls 1987), but it may be time consuming and, therefore, energetically costly (Lambrechts 1996). However, competition for resources is also an energy expenditure. The time spent competing for resources decreases the time available for increasing fitness (Ydenberg et al. 1988). If an individual can recognize another's song, then birds nearest each other may spend less time defending common boundaries. Recognition would imply awareness of the identities of other individuals and discrimination between those individuals (Stoddard 1996). Evolution of individually distinct vocalizations would benefit both the individual sending the signal and the individual receiving the signal (Bradbury and Vehrencamp 1998).

The tendency towards stable neighbor relationships with reduced aggression over time has been labeled the "dear enemy" effect (Fisher 1954). This hypothesis predicts that neighboring territorial birds show reduced aggression when a neighbor (a bird sharing a territory boundary with another conspecific) sings from his own boundary. However, when a stranger (an unfamiliar conspecific) sings from the same location it is treated as an intruder (Stoddard 1996). Getty (1989) predicted that mean duration of contests should be shorter for recognized individuals than for strangers because strangers pose a threat of usurping the entire territory rather than part of a territory or a mate. A neighbor poses the threat of gaining extra pair copulations, yet

few studies support extra pair copulations in North American owls (see Marks et al. 1999). According to Marks et al. (1999), extra pair copulations would not be evolutionarily selected for in birds where there is a high degree of male parental care, such as Northern Spotted Owls. However, several studies of passerine species have supported the “dear enemy” effect (see Falls 1992).

Recognition patterns in bird communication have been documented in many passerines (see Weeden and Falls 1959, Falls and D’Agincourt 1981, McGregor and Avery 1986, Brindley 1991). Song may provide details regarding kinship, territory boundaries, neighbor recognition, and even individual recognition. The ability of birds to recognize strangers from neighbors could be an example of associative learning for the purpose of individual recognition. For example, Falls and Brooks (1975) broadcast neighboring White-throated Sparrow’s (*Zonotrichia albicollis*) calls from non-traditional boundaries and found territory holding males treated these as unfamiliar calls. Such measurable differences detected in response to familiar birds and to familiar birds in novel locations lends support to contextual discrimination among individuals. Therefore, contextual recognition may be important in reducing escalated contests between neighbors (Ydenberg et al. 1988), which could reduce energy expenditures for territorial defense, thereby, increasing fitness.

I used playback experiments to examine the ability of male Northern Spotted Owls to recognize their neighbors. Given the “dear enemy” hypothesis (Fisher 1954), I predicted that territorial male Northern Spotted Owls would respond quicker, more frequently, and with more intensity to calls of a stranger than to those of a neighbor. I

also expected that when the locality of a neighbor call changed, e.g., to an opposing boundary, males would respond with less intensity and frequency than when responding to an unfamiliar conspecific, but more so than to a neighboring male in its typical location. I expected that territory holding birds would associate each neighbor's call with a specific locality, and if this locality changed, so might their response.

My predictions are based on data from a pilot study I conducted in 1999 as well as the "dear enemy" effect (Fisher 1954). Using an opposite neighbor test implies a contextual component and addresses the question: are birds recognizing neighbors based upon the location of a call, or are they recognizing the individual bird itself? Response variables used to test this hypothesis included latency to first response, mean time elapsed between calls, and number of calls given.

It is important to examine why individual recognition may have evolved in the social system of Northern Spotted Owls because of the role it may play in conservation strategies for this threatened species (U.S. Department of the Interior 1990). Understanding behavior in conservation efforts can be crucial to slowing the decline of many species (Ulfstrand 1996). Recognition patterns among conspecifics may reduce total energy expenditures by minimizing territorial challenges and, therefore, lead to greater overall fitness (Ydenberg et al. 1988). Higher turnover rates within territories due to habitat degradation may lead to the appearance of more unfamiliar conspecifics over time, and thus resident birds would expend more energy until recognition of a new neighbor is achieved, what I refer to as the "new neighbor

energy adjustment consequence.” The objectives of my study were to better understand the information communicated by territorial males and to determine what, if any, recognition exists between individuals sending and receiving vocal signals.

STUDY AREA

My primary research area was the 292 km² Willow Creek Study Area, near Willow Creek, California located within Humboldt and Trinity counties on the Six Rivers and the Shasta-Trinity National Forests (Figure 1). I also sampled outlying territories (regional sites) to increase my total sample size. Regional sites consisted of assemblages of established territories, outside of the Willow Creek Study Area, ranging from Siskiyou County, south to Mendicino County (Figure 1). All areas have been intensively monitored for over 18 years (see Franklin et al. 2000). Each owl was individually marked with colored leg bands to monitor the identity of birds within territories as part of a long-term demographic study (Franklin et al. 2000).

The terrain within the study area was steep and mountainous ranging in elevation from 150 m to 1,700 m (Franklin et al. 1990). Vegetation used by Northern Spotted Owls in the study area was mixed evergreen forest dominated by old growth Douglas-fir (*Pseudotsuga menziesii*) with a hardwood understory of Pacific madrone (*Arbutus menziesii*), tanoak (*Lithocarpus densiflora*), canyon live oak (*Quercus chrysolepis*), and golden chinquapin (*Chrysolepis chrysolepis*) (Küchler 1977). The climate within my study site was Mediterranean (Major 1977), with warm dry summers and cool wet winters.

Most territories consisted of previously logged forest with interspersed undisturbed primary forests that included variable levels of connectivity among stands (Gutiérrez et al. 1998). Old logging roads allowed access to the territories sampled in this study.

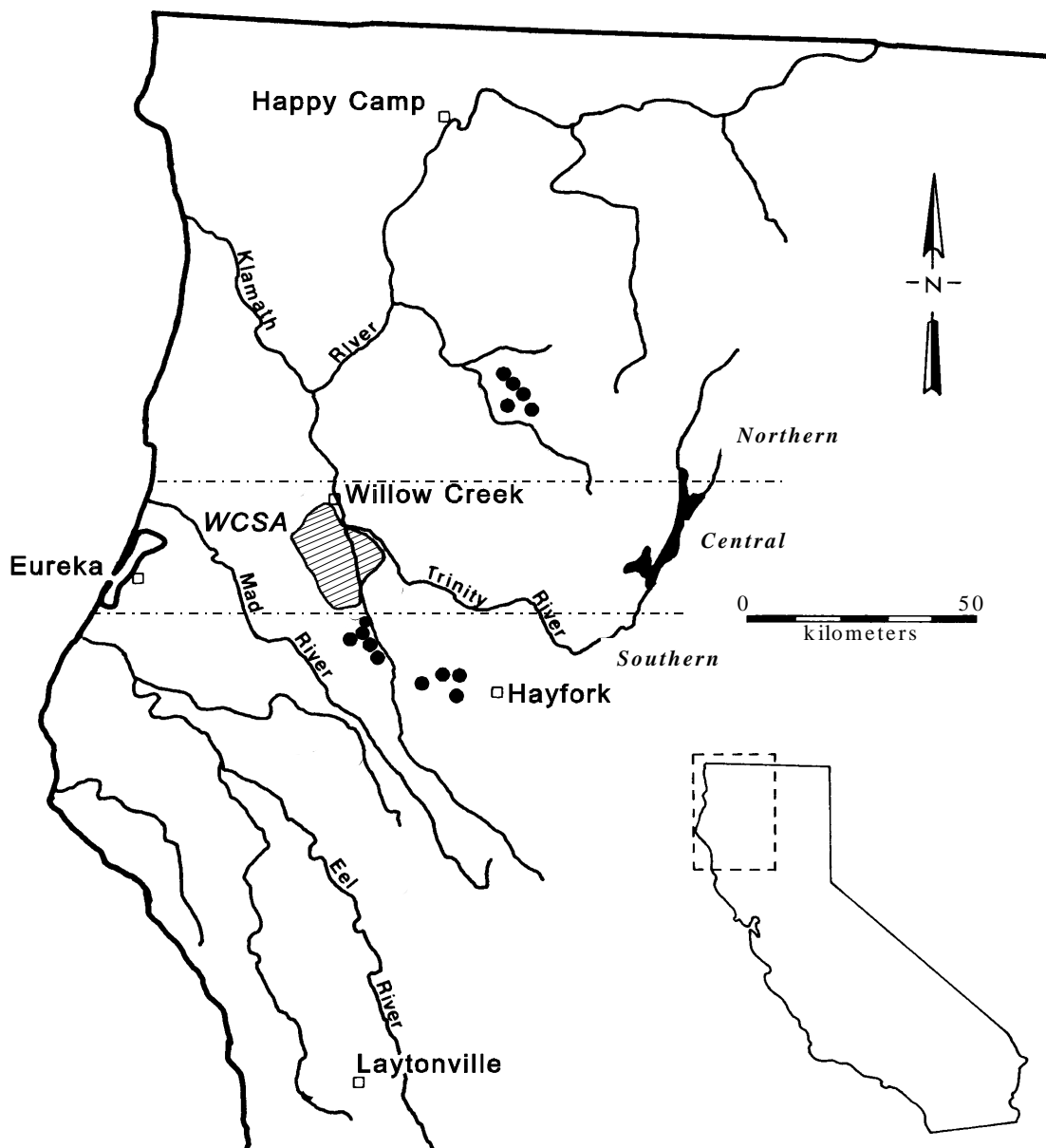


Figure 1. Map of study area in Northwestern California. Dots represent outlying territories, hatched area represents the Willow Creek Study Area, and lines separate the study groups (base map from Franklin et al. 2000).

Ninety-five territories were monitored annually: 56 territories in the Willow Creek Study Area and 39 regional territories (see Figure 1). Not all territories were occupied each year. In 1999 a total of 59 territories were occupied, in 2000 a total of 60 territories were occupied. Of these 60 territories, 34 had neighbors and were recorded for playback purposes. A subset ($n = 10$) of the 34 was used for the pilot study, and 16 territories were used in the 2000 study based on accessibility and occupancy (Table 1).

Table 1. List of territories occupied by male Northern Spotted Owls that were tested with neighboring males in 2000 (n=16), divided into 3 study groups.

Study Group	Number of Territories	Number of Territories Responding
Northern	1	1
Central	9	7
Southern	6	5
	n=16	n=13

METHODS

Pilot Study

I conducted a pilot study in August of 1999 on the Willow Creek Study Area. The purpose of this study was to test equipment and procedures, to estimate an appropriate sample size (power analysis), as well as to establish an appropriate study design. Playback tapes were created to simulate calling male spotted owls. These tapes were then broadcast in ten different territories. Each territory was tested twice from the same location, once using a neighbor call and once using a call of an unfamiliar conspecific. All responses to the playback were recorded. Of ten tested individuals, only four responded to both tests. The responses of these four territories were then used to calculate a power analysis.

Using the pilot study data, I also tested the potential correlation among four previously chosen variables: latency to first call, average time between calls, number of calls given, and calls-per-effort. I found that the variable, “calls-per-effort” was highly correlated with the number of calls given and average time between calls. The correlation coefficient for time between calls and the total number of calls variables were $r = -0.87$ for strangers and $r = -0.82$ for neighbors ($n = 4$ territories). Therefore, I discarded the “calls-per-effort” variable; and instead used total number of calls given by a male as a response variable in addition to average time between calls and latency to first call.

Response Variables

Latency

Latency to first response was the time (seconds) between the start of the playback tape and the first response heard from the tested individual. Latency to first response has been a common variable used to determine recognition (see Falls and D'Agincourt 1981, Weary et al. 1987, Galeotti and Pavan 1993). I predicted that male Northern Spotted Owls would respond slower to playbacks of a neighbor's call (N) than to a stranger's call (S), but that males would respond either more quickly or in the same amount of time to the call of a stranger than to a call of a neighbor from the opposite boundary (ON). Using the amount of time as a measure my prediction can be represented as $N > ON > S$.

Average Time Between Calls

Average time between calls was the time (seconds) that lapses between calls which may reflect some level of aggression between neighbors and strangers. An owl that responds with greater intensity may have less time between successive calls. If a male recognizes his neighbor then it would be advantageous to expend less energy by not responding. I hypothesized that male Northern Spotted Owl calls would be farther apart in time when responding to playbacks of a neighbor's call (N) than to a stranger's call (S). Likewise, responses to playbacks of stranger's calls would be farther apart or similar in distance than to neighbors from an opposing boundary (ON). The prediction for average time between calls can be represented as $N > ON > S$.

Number of Calls Given

Number of calls given during a response bout is another commonly measured variable used in playback studies (see Weary et al. 1987, Brindley 1991, Galeotti and Pavan 1993). An owl responding to a male stranger may give more calls than if he were responding to a neighbor. Thus I hypothesized that male Northern Spotted Owls would call more frequently in response to a playback of a stranger's call (S) than to a neighbor's call (N), and calling frequency to playbacks of strangers (S) would be greater than or equal to neighbors from an opposing boundary (ON); this prediction can be represented as $N < ON \leq S$.

Territory Selection

At the end of the 1999 survey season, 34 territories existed that were actively defended by males and had neighboring territories, which were also being defended. Of these territories, only those where both the original male and the neighboring male remained from the 1999 season were used for the 2000 study ($n = 16$). This selection eliminated responses that could be influenced by new neighbors who may still be considered unfamiliar by the bordering male (new neighbor energy adjustment consequence) and yet still incorporated results from the power analysis. The power analysis from the pilot study was utilized to help determine an appropriate sample size for the study design at $\alpha = 0.05$. For 92 percent power within each month, a sample size of 13 was necessary for the variable, "total number of calls given."

A smaller sample size ($n = 5$) for each month was required for 92 percent power for the variable “average time between calls.” No power analysis was completed on the latency variable as that was not tested in the pilot study.

I assumed that neighboring Northern Spotted Owls defended areas with centers averaging 710 meters from one another (Franklin et al. 2000). This distance was based on one-half the average nearest neighbor distance between territory centers from 1985 to 1994 and 2000 nest and roost sites on the Willow Creek Study Area. I defined neighbors as individuals occupying an adjacent territory for greater than one year and who also shared a common boundary with another known individual. A stranger was an individual who was unfamiliar with the bird being tested.

The entire study area was sub-divided into three sections: northern, central, and southern (Willow Creek Study Area and outlying territories combined; see Figure. 1). This division was required to ensure completely unfamiliar strangers for each test. Additionally, a minimum distance of 14 km between sub-divided sections was used to define strangers. To avoid using stranger calls that may actually have been familiar to tested owls I randomly assigned strangers to test subjects. Stranger tapes played within a territory were randomly assigned from the most logically distant recorded males within the entire study region. For example, the more northern sites had strangers assigned from the centrally located sites and the central sites were assigned strangers from the southern section. The stranger tapes came from

presumed unrelated males who may also have had different dialects (Fitton 1991). If the locality of the tested territory and the playback stranger's territory were closer than the 14 km minimum distance, the stranger was reassigned.

Playback Protocol

To test my predictions from the dear enemy hypothesis I conducted an experiment composed of two treatments (neighbor and stranger) and a control at the boundary that borders the territory of each individual. A third treatment (opposite neighbor) was conducted on the opposite boundary. The playback experiments were conducted under an approved animal research protocol (IACUC #99/00.W.95.0). Playbacks were conducted between 460 and 860 meters (a 400 m range) from known territory centers that were based on average owl locations (from 1985 to 1994) and the known 2000 locations. This range in distance was necessary to 1) allow for considerations in topography, such as ridge-lines, and 2) allow for sufficient volume for broadcasting the taped calls. The lower cutoff of 460 m also avoided playbacks within the core area surrounding a nest tree or roost site in which an owl may react more strongly to a conspecific regardless of whether it was a neighbor or stranger.

The playback station was usually within a general overlap area of the two territories of interest (Figure 2). However, each territory center was mapped *a priori* with a 710 meter circular boundary. This circle was then divided into four sections (Figure 3). Two sections were 120 degrees each, on the side facing the neighbor and on the side opposite the neighbor. The remaining 120 degrees was split into two parts. These remaining 60 degrees separated the neighbor and opposite neighbor

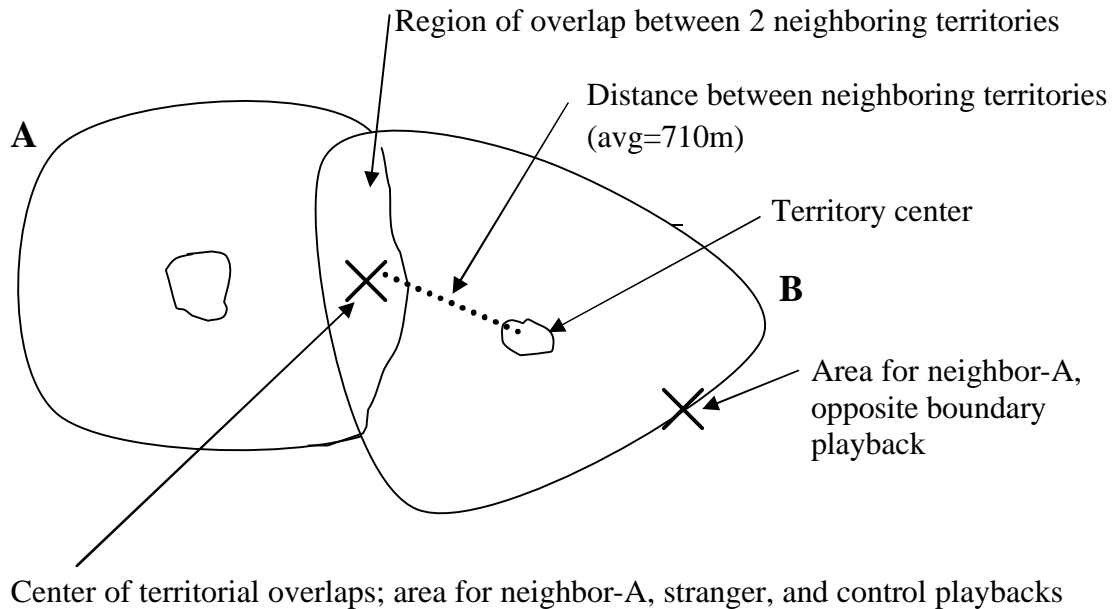


Figure 2. Schematic of playback scenario with territory-B receiving the treatments and the recorded individual from territory-A used in the playback.

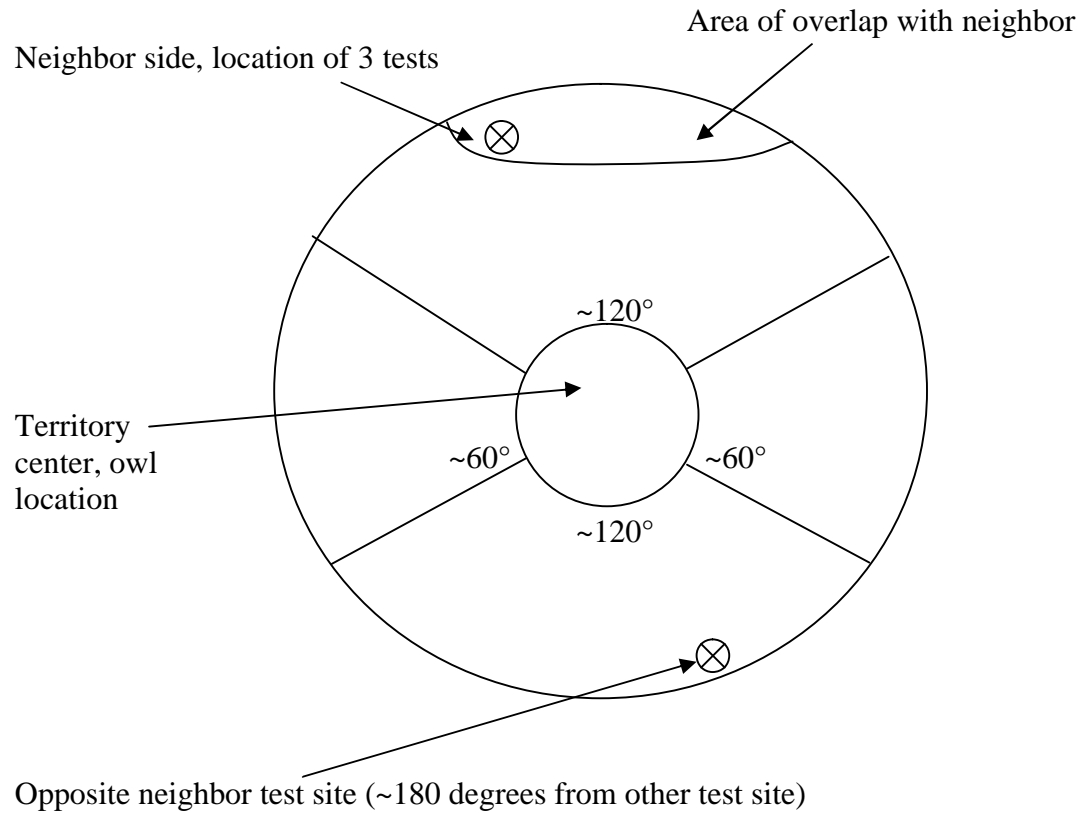


Figure 3. Example of delineating a territory into thirds for equal playback placement between all tested territories.

sides. Each of the three tests was performed on the nearest neighbor side in an area as close to, but not closer than 460 meters, the territory center for best transmission of the playbacks. An additional treatment, neighbor at the opposing boundary, was applied by playing a neighbor call on the opposite side of tested territories (i.e. a familiar call from an unexpected location). The same locality conditions from the first set of treatments applied, and the treatment was conducted roughly 180 degrees from the other test site. Each playback consisted of male four-note location calls, repeated every twenty seconds for 10 minutes followed by a 10 minute listening period. This process of playback and listening was repeated twice, for a total of 40 minutes. The average length of an owl calling bout was 9.9 minutes (Ganey 1990), and a 20 second interval between calls was based on averages (from both neighbor and stranger responses) that I estimated during the 1999 pilot study. During the 1999 pilot study, the 40 minute test length included an average of 85 percent of all calls heard. To insure similar output of all playbacks I monitored calls using a decibel meter; all playbacks were set at a volume with an average readout of 75 ± 5 dB. This range was based on measurements recorded from five calling males and was also loud enough to reach most of a tested territory.

To incorporate inherent individual variation of individuals and more adequately represent each male on a playback tape, I used multiple calls from the same individual (Kroodsma 1989). The playbacks consisted of only male four-note location calls because they have a primary function in territory defense (Forsman et

al. 1984). I used three to five different four-note location calls from the same male on each playback tape. A different set of neighbor and stranger calls was used for each territory. Thus, the sample size of playback tapes equaled the number of territories to be tested (n=16). This avoided pseudoreplication of samples and ensured independence between tests (Kroodsma 1989).

Equipment

Recordings were made using a Technics (Panasonic, Matsushita Electric Corporation of America, USA) 686D 3-head stereo cassette deck, which produced high quality sound recordings while allowing the recording to be monitored (Library of Natural Sounds 1988). This was used in conjunction with a Sennheiser (Sennheiser Electric Corporation, USA) microphone and powering module attached to a Gibson (RD Systems, Canada) 24 inch parabolic reflector for greater sensitivity and less electronic noise (Library of Natural Sounds 1988). No filters were used on any recordings. All recordings made in 1999 were used again in 2000 if the same males occupied the same territories. I assumed that there were no significant changes in an individual's call from one year to the following year.

A Sony (Sony Corporation of America, USA) TCV-5000 tape deck was used for all playbacks which was then transmitted from a Pignose (Pignose Industries, Gardena, CA) amplifying speaker for amplification purposes. The speaker was mounted onto a three-meter tall tripod and angled into the territory being tested. All owl calls heard within the 40 minute period were noted into a laptop computer using a Microsoft Excel macro. Using the macro, I recorded the time of each response, the

type of call given, sex of the bird heard calling, as well as any change in distance (intensity of call) of the responding owl. For each test, an assistant made tape recordings of male responses within the 40 minute test period.

Experimental Design and Analysis

I used a crossover experimental design with replicated blocks and analyzed my results using an analysis of variance (ANOVA) in NCSS 2000 (Jerry Hintze, Kayville, Utah) to test for differences between my four factors (Ott 1993). The four factors of interest were, season (month) and sequence (week) in which the tests are administered, within season responses to the tests (treatments), and the owls being tested (territory). The model for this design was:

$$X_{ijkl} = A_i + B_j(A) + C_k + D_l + E$$

where A is the month factor or block, B is territory nested within month, C is the treatment factor, D is the order of the treatments, and E is the error term.

The crossover design allowed for removal of nuisance factors such as season and sequence of tests, and it was the most appropriate to test the predictions. Owls were nested within test sequence and crossed with treatment. Each owl within a territory was administered three treatments, hence the repeated measures. I assumed that there were no third order interactions because repeated measures were incorporated into the design. Each of the response variables (latency to first response, mean time between calls, and number of calls given) was analyzed separately for each treatment on each individual owl. I replicated territories (the sampling unit) in

each of the three month blocks: June, July, and August. Within each month block all males received the same three treatments: neighbor, stranger, and neighbor from opposite boundary, as well as the control.

In crossover experiments there is an underlying assumption of circularity or carryover effects, in that there can be correlations among the repeated measurements (Zar 1999). This assumption suggests that the correlation between weeks one and two should be the same as the correlation between weeks one and three, and so on. Circularity or carryover effects are difficult to discern, I tried to avoid violating this assumption by including a waiting period of five to seven days between tests to prevent any habituation of the test subjects.

I computed effect sizes and 95% confidence intervals based on the Newman-Keuls multiple range test (Zar 1999) where factors were significant. Differences between multiple means were controlled for any experiment-wise error due to unequal sample sizes.

Other factors I considered included the time of night, reproductive status of the birds, and phases of the moon. Time of night was an important consideration for this nocturnal species because their activity patterns vary throughout the evening (Forsman et al. 1984). Playback experiments were conducted from sunset to three hours following sunset because male owls can move significant distances from their roost sites three hours post-sunset (Forsman et al. 1984) and because of logistical constraints in getting from one test site to another. Breeding status was not known before many tests took place and, therefore, could not be included as a block.

However, all owls tested were paired, and 12 of 13 males that responded, successfully produced young. Ganey (1990) showed that the unsolicited calling rates of the Mexican Spotted Owls (*Strix occidentalis lucida*) were related to moon phase. Owls were most vocal during the new and last quarter moon phases. Moon phase is a nuisance factor and could not be controlled in the design due to logistical constraints of sample size and biologically significant month blocks.

A post hoc analysis was conducted on the effects moon phase had on latency to first call. That time period was then compared to five phases of the moon (0-4), zero being no moon and four being a full moon. Using a large data set (n=1272) from the 1999 survey effort (see long-term demography study in Franklin et al. 2000), I could determine the effect, if any, the visible size of the moon had on call responses.

In my original design I had a balanced four-by-four crossover design with months used as a block. My intent was to incorporate the month of May as a fourth month block as well as to integrate the control into the design. However, this design could not be used in the final analysis, as there were not enough responses heard in the month of May from the tested territories. The control was completely removed from the design because of the lack of data in May, yet it was still conducted at the end of each block. To have a balanced crossover design, I included three treatments (neighbor, stranger, and opposite neighbor) and three months (June, July, and August). The control was then analyzed separately.

Controls were administered to each owl territory tested. In the control, no calls were played but the setup procedure was identical. The control test period was

also 40 minutes in duration and all calls heard were recorded into the data logger and on tape. Data collected within the controls provided background data on undisturbed calling rates for individual owls. However, the controls were not administered on a random basis. Rather, controls were given to each territory at the end of their test block. This allowed the washout period between the three treatments to remain the same throughout the testing period.

I addressed randomization and blocking in my design in several ways. The first treatment given was randomly assigned; however, to insure that there was no order effect, the order of the remaining treatments was not randomly assigned. Each block had a specific order of treatments, unlike any other block (Figure 4). To eliminate the potentially confounding effects of season, each territory was randomly assigned to a month in which all four tests were given. Sampling occurred 1 June - 15 August when the critical nesting period was over, but males still defended their territories with the four-note location call (Forsman et al. 1984). Therefore, blocking on month was crucial to the design. Blocking also reduced the error term so that more of the overall variability in the effects could be explained (Merrill et al. 2000). Within each month block, when each of the three treatments was applied, a washout period of five to seven days was used. I chose this period such that treatments were

Order of treatments

Month	June	Neighbor	Stranger	Opposite Neighbor
	July	Stranger	Opposite Neighbor	Neighbor
	August	Opposite Neighbor	Neighbor	Stranger

Figure 4. Layout of crossover design to test responses of male Northern Spotted Owls in 16 territories to different playback treatments. Each order block (columns) is identical such that the same treatments are administered (neighbor, stranger, and opposite neighbor) in each block yet each treatment order (rows) is different within each month

sufficiently separated in time so that no residual effects from one treatment carried over into subsequent treatments, but that treatments were not so far apart that subsequent detected differences could not be attributed to seasonal effects.

RESULTS

I tested 16 spotted owl territories and a total of 13 males and nine females responded to playbacks (Appendix A). Three territories were discarded completely from the analysis because there were no responses to any of the four tests, and I could not be sure if the total lack of responses was due to human error or owl behavior. Of the 13 territories used, 27 responses were noted from 48 treatments. Three males responded to only one treatment, and 10 of the tested males responded to at least two of the three treatments.

Females responded in nine of the 13 territories, and in 13 of the 39 tests. In one territory a female responded to a greater number of tests than did her mate. However, females were not used for the analysis as they gave far fewer responses in all playback treatments. Females tended to respond with crowbarks (an agitation call) or contact calls, whereas males responded with the four-note location or series location calls typical of territory defense.

Treatment Effects

Of the three response variables, latency showed a significant treatment effect (Crossover ANOVA: $F = 5.00$, $P = 0.077$). Male spotted owls responded more quickly to a stranger playback than to a neighbor playback ($\bar{x}_N - \bar{x}_S = 3.85$, 95% CI = -1.44, 9.14), providing support for the “dear enemy” hypothesis. Additionally, birds responded the slowest to a neighbor on the opposite boundary ($\bar{x}_{ON} - \bar{x}_N = 4.55$, 95%

CI = -0.74, 9.84). Hence, owls took the greatest amount of time before they responded to neighbors on the opposite boundary (Figure 5). Mean treatment effects were ordered as ON greater than N greater than S, rather than N greater than ON greater than S as predicted.

There was no treatment effect on the average time between calls (Crossover ANOVA: $F = 1.71$, $P = 0.24$). However, territory holding males seemed to take more time between vocalizations when responding to neighbors than to either a stranger or an opposite neighbor treatment ($\bar{x}_N - \bar{x}_S = 51.29$, 95% CI = -58.75, 161.33 and $\bar{x}_N - \bar{x}_{ON} = 90.79$, 95% CI = -45.56, 227.15; Figure 6). Mean treatment effects were ordered as N greater than S greater than ON, rather than the predicted ordering of N greater than ON greater than or equal to S. The mean number of calls given by territorial males was also not significant in relation to treatment effects (Crossover ANOVA: $F = 0.45$, $P = 0.643$; Figure 7). Mean treatment effects for number of calls were ordered as ON less than N less than S, rather than the predicted N less than ON less than or equal to S.

Block Effects

There was a significant month effect relative to the average time between calls (Crossover ANOVA: $F = 7.56$, $P = 0.01$). In July, birds responded with longer spacing between their calls than in either the June or August blocks ($\bar{x}_{July} - \bar{x}_{June} = 87.28$, 95% CI = 48.78, 223.34 and $\bar{x}_{July} - \bar{x}_{Aug} = 84.546$, 95% CI = -25.25, 194.35; Figure 8). The number of calls given also was reduced greatly in July ($\bar{x}_{June} - \bar{x}_{July} =$

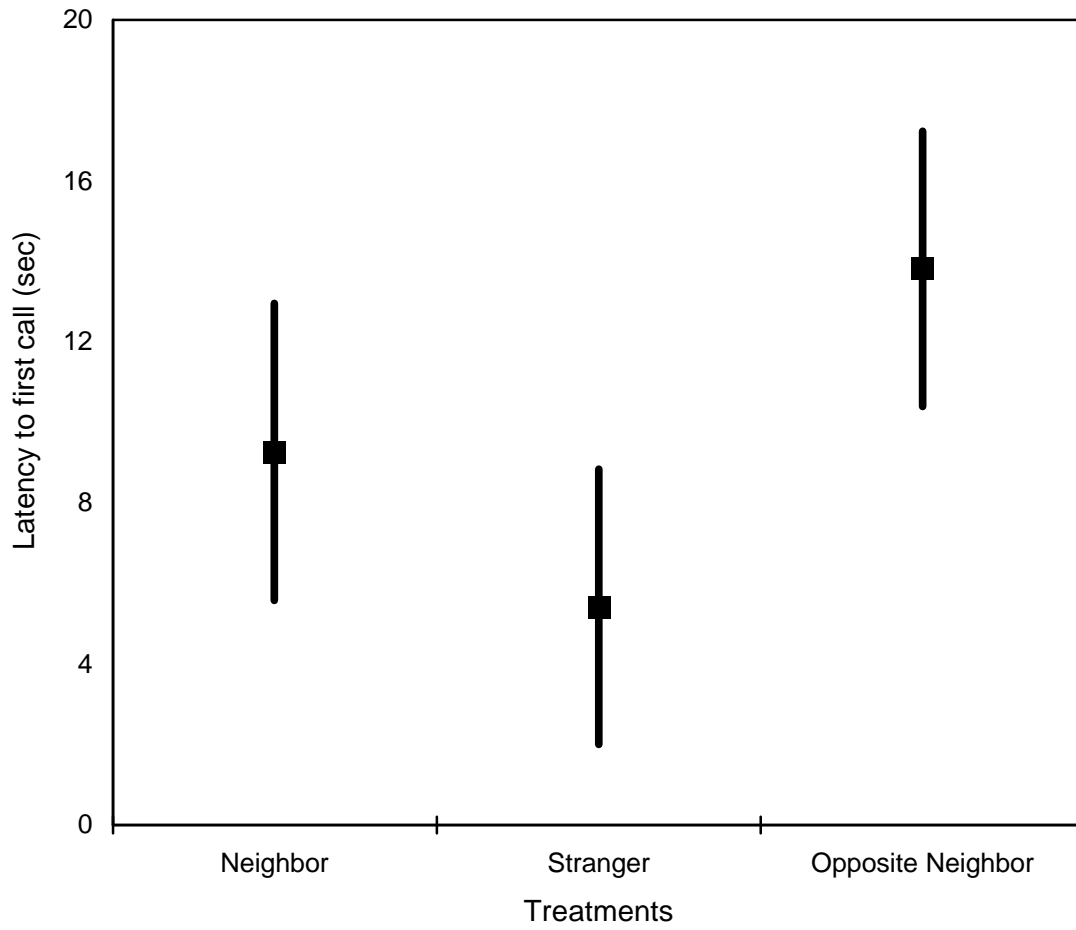


Figure 5. Effect of the three treatments on latency to first response (seconds) in male territorial Spotted Owls. Values are the means with upper and lower 95% confidence intervals

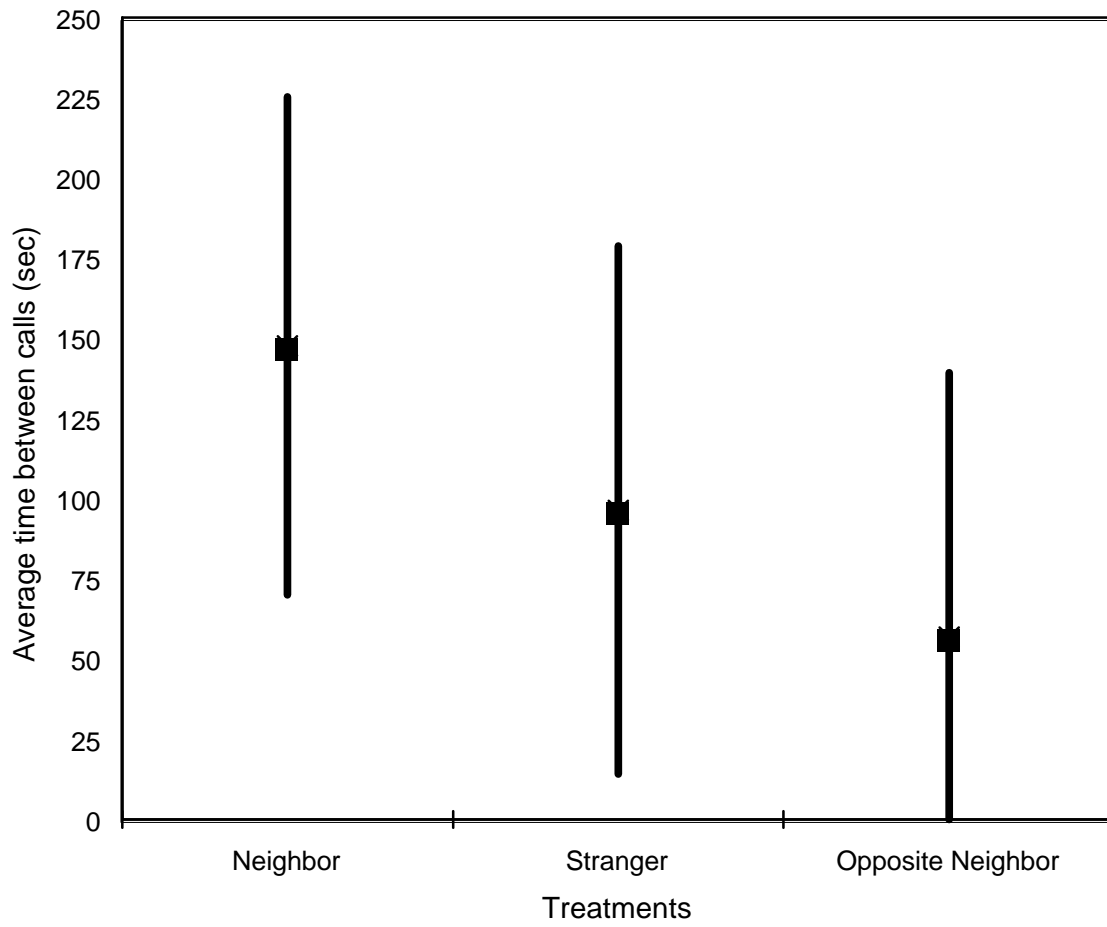


Figure 6. Effect of the three treatments on the average time between calls (seconds) in male territorial Spotted Owls. Values are the means with upper and lower 95% confidence intervals.

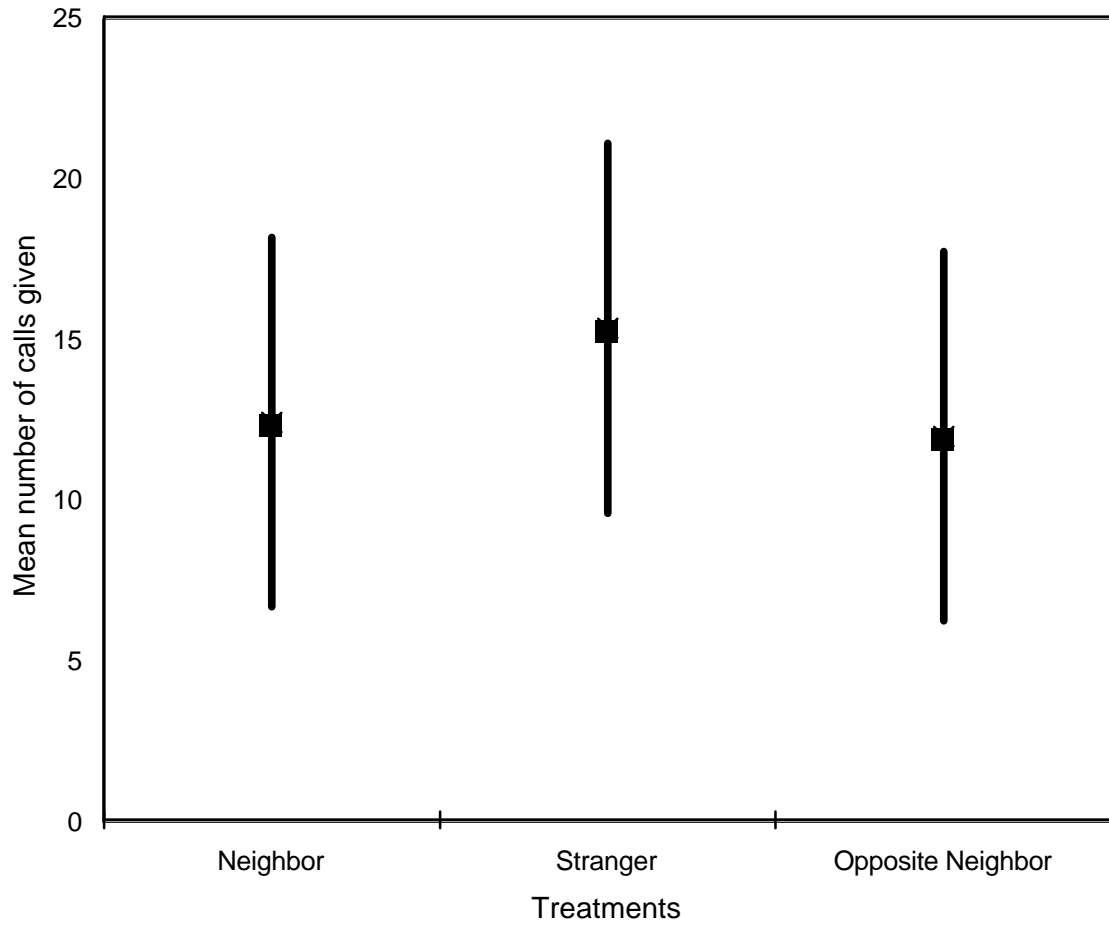


Figure 7. Effect of the three treatments on the mean number of calls given by male territorial Spotted Owls. Values are the means with upper and lower 95% confidence intervals.

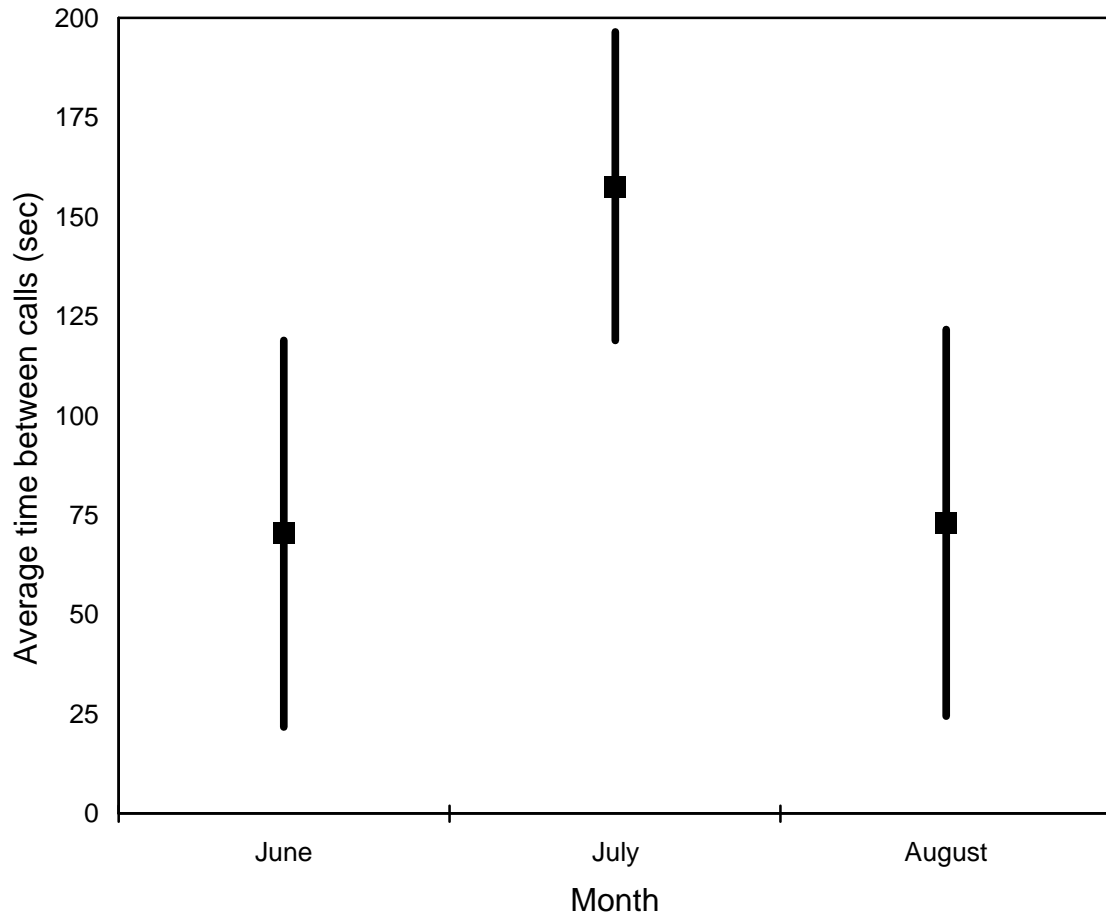


Figure 8. Effect of month on the average time between calls given by male territorial Spotted Owls. Values are the means with upper and lower 95% confidence intervals.

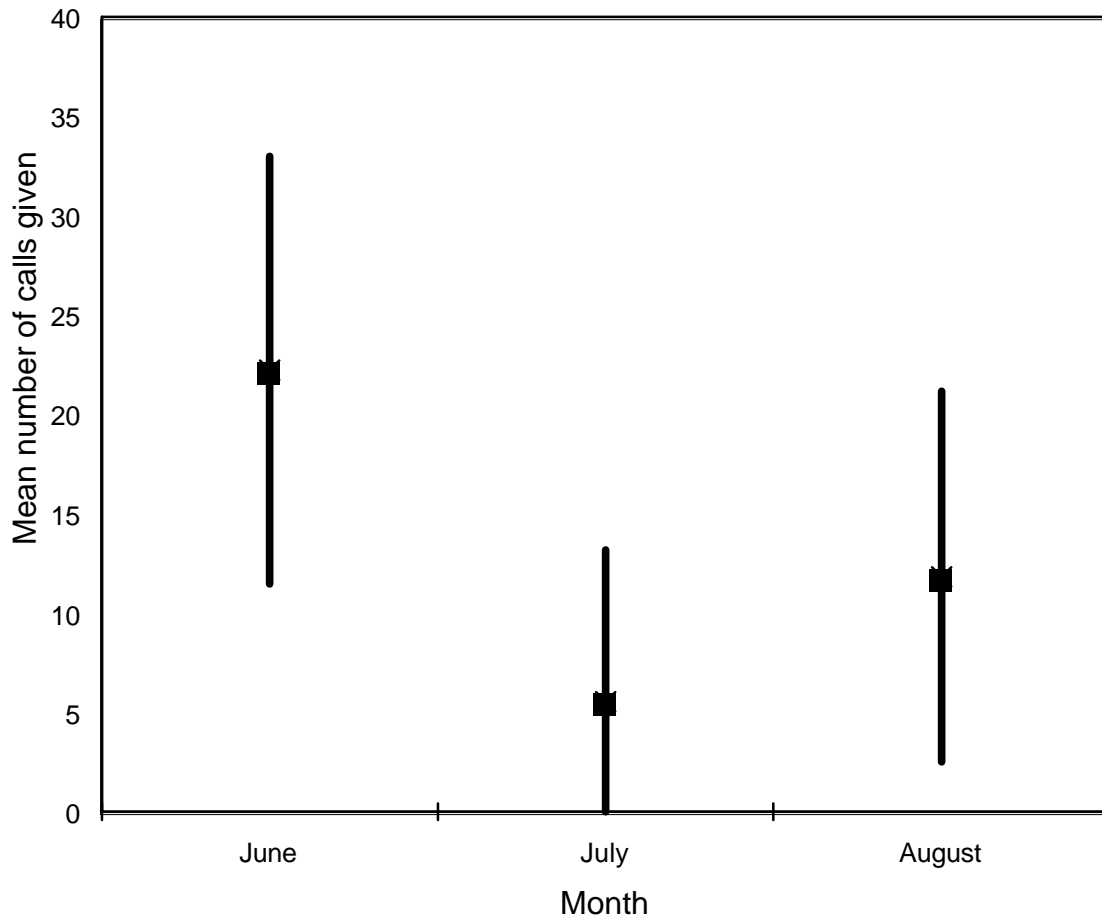


Figure 9. Effect of month on the mean number of calls given by male territorial Spotted Owls. Values are the means with upper and lower 95% confidence intervals.

16.67, 95% CI = 6.81, 26.51 and $\bar{x}_{\text{Aug}} - \bar{x}_{\text{July}} = 6.27$, 95% CI = -1.16, 13.70; Figure 9). This suggests a seasonal component to the level of intensity of responses by male spotted owls throughout the breeding months. The significance of the month block also suggests that the blocking in the crossover design was useful. Using the mean squares from the error term and that of month block (Ott 1993), the relative frequency of the blocked design for latency is 4.43 and for the mean number of calls the relative frequency is 4.8. This suggests that four times as many observations would have been required in a randomized complete block design versus a crossover design with blocks. The blocking diminished effects between subject variation, which may have been masked by the treatment effects had a crossover not been implemented. This has important implications for interpretations of past and future playback experiments (see Discussion).

A control was conducted at each territory during each month block to examine natural calling behavior during the evening hours. The control was not included in the analysis (Table 2). Only two territories of 16 responded during the control test, leaving 14 territories unresponsive during the control. One male owl responded to the calls of a nearby Great-Horned Owl (*Bubo virginianus*). The other male may have responded to human presence, which can occur in spotted owls. Nevertheless, the mean number of calls given by these two spotted owls was much lower than in the treatments.

Table 2. Means and standard errors for control calculated for each variable (n = 2).

	\bar{x}	S.E.
Latency to first call (seconds)	1.44 sec	5.19 sec
Average time between calls (seconds)	0.06 sec	0.18 sec
Mean number of calls given	1.00	3.09

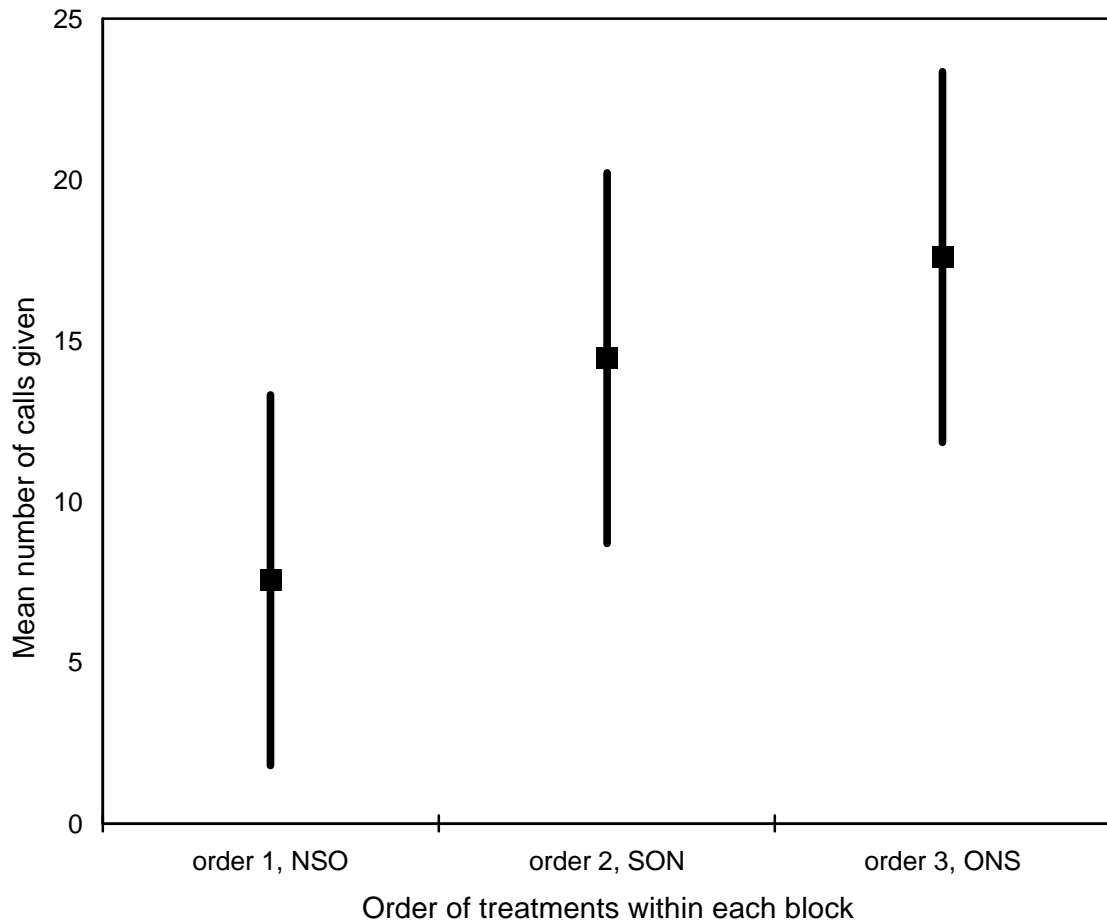


Figure 10. Effect of the order of treatments on the mean number of calls given by male territorial Spotted Owls. Neighbor test (N) was administered first in the first month block (June), followed by the stranger (S) test and finished with the opposite neighbor (O) test. Stranger test was administered first in the second month block (July), and the opposite neighbor treatment was administered first in the last month block (August). Values are the means with upper and lower 95% confidence intervals.

Carryover Effects

There was evidence of potential carryover effects in both mean number of calls given (Figure 10) and latency. Male owls tended to give more calls during the last round of treatments, despite the treatment administered (Crossover ANOVA: $F = 3.56$, $P = 0.04$; $\bar{x}_{\text{order3}} - \bar{x}_{\text{order2}} = 3.13$, 95% CI = -5.0, 11.26; $\bar{x}_{\text{order3}} - \bar{x}_{\text{order1}} = 10.03$, 95% CI = -1.18, 21.24; Figure 10). The fact that responses became more pronounced with further treatments suggested that birds were sensitized with each additional test (Hansen 1979, Falls and D'Angicourt 1981). With latency, there was a slight decrease in the time to first response throughout the test period (Crossover ANOVA: $F = 3.45$, $P = 0.08$). This also suggested some level of sensitization. There were no significant carryover effects in average time between calls (Crossover ANOVA: $F_{\text{avg timeb/wcalls}} = 0.94$, $P = 0.03$).

Jones and Kenward (1989) provided potential reasons for significant carryover effects. They also noted that significant carryover effects can affect the magnitude of the treatment effects (Jones and Kenward 1989). One potential problem with my subjects was that carryover effects were psychological, in which the subject's responses were dependent on the first round of treatments. This is supported by the reaction threshold theory (Hansen 1979, Falls and D'Angicourt 1981). Another possibility is that there was a direct-by-period interaction (Jones and Kenward 1989) in which the owl responses differed in time or the period in which the treatments were

received. This is discussed further in terms of temporal calling patterns in the discussion.

Moon Phase

To help determine whether the visible phases of the moon played a role in my results, I conducted a post hoc analysis. In this analysis, I compared the difference in time between when a calling point survey began and when an owl responded from data among moon phase groups gathered in 1999. Moon phase did not significantly effect the time to first response (ANOVA: $F = 0.51$, $P = 0.726$).

DISCUSSION

Spotted owls responded more quickly to calls of an unfamiliar owl than to calls of a familiar owl. The observed differences in latency lends support to the “dear enemy” hypothesis (Fisher 1954), although not completely in the manner I originally predicted. The result makes energetic sense considering that spotted owls exhibit high site fidelity and have the largest average annual home range relative to their weight among North American owls (Johnsgard 1988). This result also suggests that there should be some adaptive advantage in call discrimination to aid territory defense of birds with large home ranges relative to body size. Using vocalizations, instead of movements to confront intruders, should aid in the effective management of energy expenditures by individuals.

It has been suggested that size or metabolic requirements of an animal are directly related to the size of the area in which it lives (Baker and Mewaldt 1979, Lindstedt et al. 1986, Reiss 1988). Birds are more metabolically constrained by the requirements of flying when compared to a mammal of similar size (Maurer 1998). The high energetic costs of flying leaves less energy for reproduction, especially for larger-bodied birds (Maurer 1998). The home range of an animal is not only a function of prey and suitable nest site density, but also a function of metabolic needs and body size.

Only latency to first response was appreciably different among the three treatments. Latency may be one cue to avoid or promote territorial disputes. Birds may keep their calling rates and cadence the same despite the identity of the signaler.

However, how quickly they advertise may indicate ownership of a territory and possibly even health of the signaling individual (Galeotti and Pavan 1993) without having to expend more energy displaying the information. For spotted owls, latency may change with recognition of the signaler, but duration or intensity of calls may not necessarily change. Galeotti and Pavan (1993) reported similar results with male Tawny Owls (*Strix aluco*) even though this species has a very small home range relative to the Northern Spotted Owl.

If males associated calls of their neighbors with specific territorial boundaries alone then I would expect a different response when neighbors were played from an opposite location than when the calls were played from the correct location. This was the case here and, therefore, I suggest that there may be individual recognition based on location. My results suggest there is a contextual component in discrimination between birds in addition to using vocal characteristics to determine their level of response to signaling conspecifics.

Unlike most of my original predictions, I found that the neighbor played from an opposite boundary did not elicit responses similar to those of strangers nor to neighbors at the correct boundary. Instead, birds refrained from responding the longest to calls of their neighbor from the opposing side. My original prediction suggested that males would respond the greatest (in time between calls, number of calls given, and latency to first call) to the most unfamiliar owl, the stranger. I suspected that the results would taper, as the owl being played back became more familiar in location and voice to the territory holding male. The slowest response was

given to the neighbor from an opposite boundary playback. Here, I hypothesize that there may be a “confusion effect.” A familiar owl calling from an unfamiliar location may be a source of confusion to a territory holding male. A male accustomed to hearing a neighbor from one location and instead hearing it from the opposite location may cause a delayed response based on uncertainty about the identity of the individual calling. The confusion effect would be a result of hearing familiar vocalizations from an unfamiliar location; a tested subject may take more time interpreting the vocalization and then choosing how to respond. The fact that the males took longer to respond to their opposite neighbor tests, but once they responded it was with greater intensity (e.g., with calls spaced closer together), may have a direct relationship with resource competition (e.g. mates). A familiar intruder may be trying to sneak resources, including extra-pair copulations. No work has been conducted on extra pair copulations within the spotted owl. However, work with other birds may suggest that perceived truces among neighbors may not withstand the test of evolution and increasing individual fitness (Black 1996).

Average time between calls was different among the monthly blocks. The use of a crossover design helped to separate out seasonal effects on spotted owl calling rates and allowed for a more direct comparison of the treatment effects. Cadence changed and birds called more slowly in the month of July and faster in June and August. Birds gave fewer calls and responded more quickly to calls during the month of July. This suggests that there are some naturally occurring temporal patterns that influence calling rates throughout the year. In June the female is typically attending

the nest, whereas July is generally when new young leave the nest, and dispersal may begin as early as late August (Gutiérrez et al. 1995). The reduced calling in July may be a safeguard to help protect newly fledged young. Responding more frequently to a conspecific during this time in the breeding season could potentially lead to greater predation rates on the vulnerable young by location announcement.

Lack of responses (22 of 48) at some territories in my study could have been a result of a distance effect. Galeotti and Pavan (1993) had similar results (50% response rate). The spatial scale of my study needs to be considered, especially in reference to other playback study designs and results. Galeotti and Pavan (1993) found distinct discrimination between familiar and unfamiliar Tawny Owls. However, the Tawny Owls they studied had reported home range of 6.0 to 32.2 ha (Galeotti and Pavan 1993) compared to 190 - 680 ha for Northern Spotted Owls (Solis and Gutiérrez 1990). In studies of passerine birds that support neighbor-stranger discrimination (Weary et al. 1987, Brindley 1991), territories are much smaller. Although great care was taken to conduct the playback studies within the core use area, playbacks may not have broadcast to owls in the manner I expected. In addition, spotted owls can forage long distances from their core area for short time periods (Forsman et al. 1984). This could have placed them out of auditory detection range in mountainous terrain. The structure of the habitat and vegetation also may have influenced the calls I transmitted and could have caused sound degradation over longer distance (Wiley and Richards 1982). Also, 12 of 13 territories had nests and the playback locations were based on multiple years of locations and not just nests of

the 2000 season. The distance from each playback to the nest may have been a factor in my response rates (Temeles 1994). Such distance effects would not only affect the ability of the owl to detect the playback, but may have also affected my ability to detect their responses.

Implications for Future Experimental Designs

Moon phase has been shown to affect calling rates of many owl species (Takats and Holroyd 1997), and calling rates can be higher during the breeding season (Bosakowski 1987). Controlling for moon phase can be difficult. I suggest in similar studies conducted in the future on nocturnal species, that each block incorporate all phases of the moon. This would not only make each month block biologically significant in terms of breeding biology, but also behaviorally significant in terms of potential effects of moon phase on calling rates. However, such a design would greatly increase logistical problems and increased sampling, especially for a species such as the spotted owl.

A post-hoc analysis on visible phases of the moon suggested that owls were not subjected to influence by the moon. These results are different than the results reported by Ganey (1990). However, because the analysis was conducted post-hoc on the previous years data and because the blocking factors were not incorporated I feel that these results must be interpreted with caution.

When conducting a playback experiment it is important to consider which variables to test. The ones I chose were most appropriate considering logistical constraints (large territories and tests conducted in the evening). Although little is

actually known about the individual call discrimination processes (Lambrechts and Dhondt 1995), White-throated Sparrows were found to recognize neighbors by the frequency or pitch of the first three notes of a song (Brooks and Falls 1975). Galeotti and Pavan (1993) used latency as well as type of behavior, type of call, and frequency to examine individual recognition in Tawny Owls. However, I feel that their findings may have been substantially different had they considered blocking and controlling for extraneous sources of variation, such as season, breeding status, and moon phase. They did find that the order in which treatments were presented (neighbor or stranger first) made no difference in the responses received, but that the preceding treatments had carryover effects into the following ones (Galeotti and Pavan 1993). I suggest that a longer washout period between successive tests may have been helpful.

My results are considerably different than many previously published playback experiments. The difference lies in my use of a crossover design. I suggest that both time of the year (month) and the order of treatments (week) influenced the response rates, and both of these factors should be incorporated into future playback designs. The overall design scheme, that of a crossover, also aided the interpretation of the results more clearly by separating out the effects of time of year. Without blocking on extraneous sources of variation that affect calling behavior, spurious treatment effects may result (Zar 1999). Therefore, time of year and order of treatments may play a large role in the outcomes of any playback experiments and should be considered in future experimental designs. Further, past results of playback studies also should be reconsidered with these thoughts in mind.

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Appendix A. Respondents for each individual territory and treatment, grouped by month.

	Territories	Neighbor	Stranger	Opposite Neighbor
<i>June</i> (NSO Order)	MADCS	0	male	male
	LAKMS	male	0	male/female
	GROUS	male	male/female	male
	AMMOC*	0	0	0
	CEDAR*	0	0	0
<i>July</i> (SON Order)	GRAPE	male	0	male/female
	MONRO	male	male	0
	CHINA	male/female	male/female	0
	GRAYR	male	0	male
	PANTH	male	male	male
	GRAYC	0	0	male
	BOISE*	0	0	0
<i>August</i> (ONS Order)	CALLA	male/female	male/female	male/female
	DRINK	male	male	0
	OAKKC	female	male	0
	MAHAL	male/female	0	0

* Denotes territories which were discarded due to lack of response