THE JOURNAL OF RAPTOR RESEARCH

A QUARTERLY PUBLICATION OF THE RAPTOR RESEARCH FOUNDATION, INC.

VOL. 39 | JUNE 2005 | NO. 2

J Raptor Res. 39(2):111–118

THE EFFECT OF BROADCASTING GREAT HORNED OWL VOCALIZATIONS ON SPOTTED OWL VOCAL RESPONSIVENESS

MICHELLE L. CROZIER, MARK E. SEAMANS, AND R.J. GUTIÉRREZ[1]

University of Minnesota, Department of Fisheries, Wildlife, and Conservation Biology, 200 Hodson Hall, 1980 Folwell Avenue, St. Paul, MN 55108 U.S.A.

ABSTRACT.—One hypothesis advanced for the association of Spotted Owls (*Strix occidentalis*) with mature forest has been avoidance of competitors and predators such as Great Horned Owls (*Bubo virginianus*). Great Horned Owls also have been identified as an issue of concern for the conservation of Spotted Owls. Thus, knowledge of Great Horned Owl presence in Spotted Owl territories could be valuable when evaluating trends in Spotted Owl survival. If Spotted Owls avoid Great Horned Owls because of risk of predation, we hypothesized that Great Horned Owl vocalizations should affect Spotted Owl calling behavior. Therefore, we experimentally examined vocal responsiveness of male Spotted Owls after Great Horned Owl vocalizations were played in their territories. We found little evidence that broadcasting Great Horned Owl vocalizations in Spotted Owl territories affected relatively short-term (24 hr) responsiveness of male Spotted Owls. Heterospecific response rates were also low for both species. Thus, our prediction that the presence of Great Horned Owls (i.e., simulated calling by Great Horned Owls) would affect Spotted Owl responsiveness was not supported, at least on the temporal scale at which we conducted the experiment. Our results suggested that surveys to estimate Great Horned Owl presence on Spotted Owl study areas would not confound surveys for Spotted Owls in those areas if at least 24 hr passed between surveys for each species.

KEY WORDS: *Great Horned Owl;* Bubo virginianus; *California Spotted Owl;* Strix occidentalis occidentalis; *cross-over experiment; heterospecific response; territoriality; auditory survey.*

EL EFECTO DE EMITIR VOCALIZACIONES DE *BUBO VIRGINIANUS* SOBRE LA RESPUESTA VOCAL DE *STRIX OCCIDENTALIS*

RESUMEN.—Se ha hipotetizado que la asociación de *Strix occidentalis* con el bosque maduro se da para evitar competidores y grandes depredadores como *Bubo virginianus. B. virginianus* también ha sido identificado como un tema de preocupación para la conservación de *S. occidentalis.* De este modo, el conocimiento de la presencia de *B. virginianus* en los territorios de *S. occidentalis* podría ser valioso al momento de evaluar las tendencias en la supervivencia de *S. occidentalis.* Si *S. occidentalis* evita a *B. virginianus* por el riesgo de depredación, hipotetizamos que las vocalizaciones de *B. virginianus* deberían afectar el comportamiento de llamada de *S. occidentalis.* En consecuencia, examinamos de modo experimental la respuesta vocal de los machos de *S. occidentalis* luego de emitir en sus territorios vocalizaciones de *B. virginianus.* No encontramos evidencia sustancial de que emitir vocalizaciones de *B. virginianus* en los territorios de *S. occidentalis* afectó la respuesta de corto plazo (24 hr) de los machos de *S. occidentalis.* Las tasas heteroespecíficas de respuesta fueron también bajas para ambas especies. De este modo, nuestra predicción de que la presencia de *B. virginianus* (i.e., la simulación del llamado de *B. virginianus*) afectaría la respuesta de *S. occidentalis* no fue avalada, al menos a la escala temporal a la cual condujimos el experimento. Nuestros resultados sugieren que los relevamientos para estimar la presencia de *B. virginianus* en las áreas de estudio de *S. occidentalis* no afec-

[1] Email address: gutie012@umn.edu

tarían los relevamientos de *S. occidentalis* en estas áreas si han pasado al menos 24 hr entre los relevamientos para cada especie.

[Traducción del equipo editorial]

One hypothesis posed for Spotted Owl (*Strix occidentalis*) habitat selection is that they use mature forest to avoid Great Horned Owls (*Bubo virginianus*), which are considered competitors and predators of Spotted Owls (Carey 1985, Gutiérrez 1985). Forsman et al. (1984, 2002) also hypothesized that Spotted Owls avoided open areas to reduce the risk of predation by Great Horned Owls. Although little evidence exists to support this hypothesis, spatial segregation and differences in habitat use may occur between the two species (Phillips et al. 1964, Johnson 1993, Ganey et al. 1997). In addition, Ganey et al. (1997) found considerable overlap in home ranges between Great Horned Owls and Mexican Spotted Owls (*S. o. lucida*), but they noted that overlap within individual forest stands was limited. Spatial segregation also has been observed between Great Horned Owls and other owls. For example, Baumgartner (1939) hypothesized that the presence of Great Horned Owls, which are competitors and predators of both Barn Owls (*Tyto alba*) and Barred Owls (*Strix varia*), restricted these latter owls to "less favorable" home ranges. Other studies have supported Baumgartner's hypothesis (Barn Owl, Rudolph 1978; Barred Owl, McGarigal and Fraser 1984). Despite some evidence for spatial segregation, Great Horned Owls are often found near Spotted Owls and the two species can have overlapping home ranges (Forsman et al. 1984, Johnson 1993, Ganey et al. 1997, pers. obs.).

Despite the potential for interspecific interactions, the effect of Great Horned Owl calling activity on the subsequent responsiveness of Spotted Owls remains unexplored. The listing decision for the northern Spotted Owl (*S. o. caurina*) identified Great Horned Owls as a threat of unknown magnitude to the Spotted Owl (USDI 1990). Subsequently, concerns for the conservation of the Spotted Owl have led to conservative Spotted Owl survey protocols. For example, current U.S. Forest Service survey protocol recommends skipping survey stations where known predators are active, including Great Horned Owls (USDA Forest Service 1993). Because the Great Horned Owl is considered a potential threat to the Spotted Owl, it would be desirable to monitor Great Horned Owl distribution and abundance within Spotted Owl demographic study areas. However, we do not know how surveys for Great Horned Owls might affect Spotted Owl detection probabilities during subsequent Spotted Owl surveys. Thus, such critical information is needed before attempting simultaneous surveys of these species in the same area.

In general, interspecific territoriality has been inferred from observation of agonistic behavior and response to song between two or more species (e.g., Orians and Willson 1964, Møller 1992). Because Great Horned Owls are predators of Spotted Owls (Forsman et al. 1984, Miller and Meslow 1985, Johnson 1993, Gutiérrez et al. 1995), we hypothesized that Spotted Owls should actively avoid them. Therefore, we predicted Great Horned Owl vocalizations would suppress Spotted Owl vocal responsiveness, including their subsequent vocal responsiveness to conspecific calls. We tested this prediction experimentally by exposing male California Spotted Owls (*S. o. occidentalis*) to calls of Great Horned Owls in order to evaluate whether we could conduct surveys of Great Horned Owls on our Spotted Owl study area while not lowering subsequent detection probability of Spotted Owls.

METHODS

Study Area. Our study was located in the central Sierra Nevada, California U.S.A. The owls we studied in this experiment were adjacent to the Eldorado Density Study Area (EDSA), the site of a long-term Spotted Owl population study (Seamans et al. 2001). Elevation at Spotted Owl territories ranged from 930–1855 m, and vegetation was typical of middle elevation Sierran Montane Forest (Küchler 1977). Prior to conducting the experiment, we established the presence of Spotted Owls within treatment and control areas by conducting surveys using standard methods (Forsman 1983, Franklin et al. 1996). During these surveys, we detected nine pairs and one single male defending territories at the experimental territory sites.

Experimental Design. We used a 2 × 2 binary cross-over experimental design (Senn 1993) to test the short-term effect of Great Horned Owl calls (i.e., simulated presence) on male Spotted Owl responsiveness. To simulate Great Horned Owl calling, we broadcast recorded calls of Great Horned Owls in 10 occupied Spotted Owl territories (see Morrell et al. 1991).

Cross-over design. We considered each male Spotted Owl as an experimental unit, Great Horned Owl calling as the treatment, and male Spotted Owl responsiveness as the dependent variable. Our cross-over design consisted of

(1) randomly applying treatments during the first time period of the experiment to half the experimental units and using the other half as controls, then (2) switching treatments and controls for the second time period (Senn 1993). Thus, after the treatment of Great Horned Owl calling was applied (Treatment Day I), we measured responsiveness of Spotted Owls to conspecific calls (Treatment Day II), compared to a control Spotted Owl survey, to test if simulated Great Horned Owl presence (i.e., broadcast calls) had an effect on Spotted Owl responsiveness. This design allowed us to use individual owls as their own controls, thus controlling for variation among experimental units (Ratkowski et al. 1993, Senn 1993). We only used Spotted Owl males because they are more vocally responsive than females (Reid et al. 1999).

We defined "short-term effect" as the effect of waiting for a 24-hr interval between Great Horned and Spotted Owl surveys. We selected a 24-hr interval to assess the efficacy of surveying for Great Horned Owls in Spotted Owl territories and, secondarily, to assess interspecific interaction at a temporal scale we felt would minimize predation risk to Spotted Owls (see below). First, we were interested in determining whether surveying for Great Horned Owls would bias the results of Spotted Owl surveys. Because Great Horned Owls have been considered a potential threat to northern Spotted Owls (USDI 1990), we wanted to estimate the distribution and abundance of Great Horned Owls on our study area, but not at the cost of disrupting our long-term Spotted Owl study. Thus, the question we tested was—do call surveys for Great Horned Owls cause Spotted Owls to reduce their responsiveness to standard survey protocol for the latter species? Concern about these species' interactions is clearly expressed in current U.S. Forest Service survey protocol for Spotted Owls, which instructs observers to note predators when detected, including Great Horned Owls, and to skip survey stations where predators are detected (USDA Forest Service 1993). Therefore, because we did not know enough about the ecological interactions between these two species to predict accurately what might be an appropriate stimulus-response interval and because the Spotted Owl is of great conservation concern, we selected a conservative 24-hr lag period to evaluate the response. That is, we did not want to follow a Great Horned Owl broadcast immediately with a Spotted Owl survey because of the potential predation risk to the latter species. In addition, an immediate progression of both species' calls may have had a confounding effect on estimated response rates (i.e., we would not know whether the Spotted Owl was responding to the Great Horned Owl call or the subsequent Spotted Owl call). We deliberated the issue of the appropriate stimulus-response period at great length prior to executing the experiment. Thus, we recognized that inferences about behavioral responses *per se* (i.e., suppression of Spotted Owl calling activity) would be limited. However, we felt that this period would be appropriate to answer our most important question regarding conducting surveys for both species on the same study area.

Logistic constraints dictated the order in which territories were visited during a survey period (i.e., territories in the same area were surveyed on the same night). However, all territories were randomly assigned initially to treatment or control groups. All territories were surveyed over nine consecutive nights during the first experimental period, followed by an 8-d pause. Treatments were reversed and territories were surveyed again within nine consecutive survey nights during the second period. The survey order that we established for the first experimental period was followed in the second experimental period so that an approximately equal amount of time (17 d) elapsed between complete treatment and control surveys in each territory. Territories took one extra day to survey in second round due to field conditions.

Broadcast call experiment. We used methods outlined by Forsman (1983) and Morrell et al. (1991) to survey for Spotted and Great Horned Owls, respectively. Within each Spotted Owl territory, we established six call points 0.4–0.6 km apart to attain complete coverage (Forsman 1983) of the area in which we had first detected each owl. We defined a complete survey as the combined results of all individual call points from one survey period within a territory (Forsman 1983). At each point, we broadcast a Great Horned Owl call or imitated a Spotted Owl call for 10 min and recorded responses by species. Spotted Owl calls were produced vocally to be consistent with methods used for the demography study. Complete surveys were conducted from 2000–0100 H PST to limit within-night variation in responsiveness (Forsman 1983). We did not conduct surveys if wind was >12 km/hr or it was raining (Forsman 1983, Morrell et al. 1991).

We structured Great Horned Owl surveys to be similar to Spotted Owl surveys. During Great Horned Owl treatments (Treatment Day I), we broadcast a recording of a male and female Great Horned Owl engaged in a calling bout (Stokes et al. 1999). For Great Horned Owl treatments only, observers listened for the first min and the last 3 min for unsolicited calls (Morrell et al. 1991, Johnson 1993). For the remainder of the survey (min 2–7), we played six Great Horned Owl broadcasts, consisting of six sets of 20-sec, 4–7 note calls by a pair of Great Horned Owls separated by a 40-sec interval. The first 20-sec broadcast was made with the speaker perpendicular to the road, then rotated 180° following each 20-sec broadcast. During Spotted Owl treatments (Control and Treatment Day II), observers vocally produced Spotted Owl calls for the entire 10 min, imitating 3–5 four-note location calls every 15 sec (Forsman 1983). The 20-sec and 15-sec intervals of silence between Spotted and Great Horned Owl calls represented the frequency of unsolicited calls observed in the field for each species (Spotted Owls: Forsman et al. 1984, Johnson 1993; Great Horned Owls: Houston et al. 1998).

A positive treatment response included any complete survey (i.e., calling at six survey points) in which a male Spotted Owl was detected during Spotted Owl broadcasts (Treatment Day II or Control). If a Great Horned or Spotted owl of either sex was detected at any survey point, observers noted time of detection, owl species, sex (based on pitch of call; Great Horned Owl: Miller 1930; Spotted Owl: Forsman 1983), response type (visual or vocal), compass estimated direction and distance to the owl, and whether the response occurred during pre-broadcast, broadcast, or post-broadcast time periods (Morrell et al. 1991). We considered a Great Horned Owl

Table 1. *A. priori* models used to evaluate the effects of treatment (broadcasting Great Horned Owl calls) and presence of Great Horned Owls (GHOW) on short-term responsiveness of male Spotted Owls (SPOW). All models are Generalized Linear Mixed Models (GLMMs) in which individual owl (SPOW) has been blocked as a random variable and all other variables have fixed effects. T, P, C, and GHOW indicate Treatment, Period, Carryover, and Great Horned Owl covariates, respectively. Intercept is included as a parameter in each model.

MODEL	MODEL STRUCUTURE	MODEL DESCRIPTION	K[a]
$M_{()}$	β_0	$SPOW_{(Random)}$	2
M_T	$\beta_0 + \beta_1$ (T)	$Treatment_{(Fixed)} + SPOW_{(Random)}$	3
M_{T+P}	$\beta_0 + \beta_1$ (T) $+ \beta_2$ (P)	$Treatment_{(Fixed)} + Period_{(Fixed)} + SPOW_{(Random)}$	4
M_{T+C}	$\beta_0 + \beta_1$ (T) $+ \beta_2$ (C)	$Treatment_{(Fixed)} + Carryover_{(Fixed)} + SPOW_{(Random)}$	4
M_{GHOW}	$\beta_0 + \beta_1$ (GHOW)	Great Horned $Owl_{(Fixed)} + SPOW_{(Random)}$	3
M_{T+GHOW}	$\beta_0 + \beta_1$(T) $+ \beta_2$ (GHOW)	$Treatment_{(Fixed)}$ + Great Horned $Owl_{(Fixed)}$ + $SPOW_{(Random)}$	4
$M_{T\times GHOW}$	$\beta_0 + \beta_1$ (T) $+ \beta_2$ (GHOW) $+ \beta_3$ (T $\times$ GHOW)	$Treatment_{(Fixed)}$ + Great Horned Owl $_{(Fixed)}$ + $SPOW_{(Random)}$	4

[a] K = number of parameters in model.

present within a Spotted Owl territory if we detected it at any point during the study.

Statistical Analysis. During our experimental design phase, we developed six *a priori* hypotheses (models) to explain how broadcasting Great Horned Owl calls might affect short-term responsiveness of male Spotted Owls (Table 1). During the data collection phase, we detected more Great Horned Owls than we expected, so we developed another model prior to analysis that included a covariate representing the detection of a Great Horned Owl(s) at a territory during a survey (i.e., a Great Horned Owl was actually present, not just simulated). We considered our seven models as competing hypotheses (Burnham and Anderson 1998). We included the individual owl as a random effect in all models. We considered treatment (T), detection of a Great Horned Owl(s) during broadcasts (GHOW), and structural components of the study design as fixed effects. Structural components of the study design included a carryover and period effect. We analyzed data within a maximum likelihood framework using a Generalized Linear Mixed Model (%GLIMMIX; SAS 8.02, SAS Institute 2001) with a logit link and binomial error because our response variable was binary (no response = 0, male Spotted Owl vocal response = 1). We used maximum likelihood estimators (MLEs) to determine parameter estimates of fixed variables (Littell et al. 1996).

We objectively ranked models using a bias-corrected version of Akaike's Information Criterion (AIC_C and ΔAIC_C; Akaike 1973, Burnham and Anderson 1998). All models were compared to a means-only model (no fixed effects). We used Akaike weights (w_i) to estimate the likelihood of each model relative to competing models, given the data (Akaike 1973, Burnham and Anderson 1998). An Akaike weight (w_i) is the weight of a specific model, defined as EXP $\{-0.5\ \Delta AIC_C\}$ of that specific model divided by the sum of (EXP$\{-0.5\ \Delta AIC_C\}$) for all models (Burnham and Anderson 1998).

We calculated an intercept, parameter estimates, and associated standard errors for fixed effects used in each of the models (Littell et al. 1996). The sign of the estimate indicated whether the variable had a positive or negative effect on Spotted Owl responsiveness. If the 90% confidence interval for a parameter estimate did not include zero, we concluded that the parameter estimate was different from zero. Therefore, if this result occurred for the treatment parameter, we inferred that Great Horned calling had an effect on Spotted Owl responsiveness.

RESULTS

We conducted our experimental study from 16 July–8 August 2003 following preliminary surveys that occurred in late June to locate occupied territories. Spotted Owl responsiveness was similar between treatment (Treatment Day II) and control surveys (Fig. 1). Although we only included male Spotted Owl response in our models, we recorded responses from both species for both sexes. Spotted Owl response rates (control = 70%, treatment = 60%) were similar to the response rate (57.3%, SE = 7.5) of Spotted Owls occupying established territories on the EDSA (R.J. Gutiérrez unpubl. data). Of 30 complete surveys (10 Control, 10 Treatment Day I, 10 Treatment Day II), Spotted and Great Horned owls were detected together during the same survey only once.

Overall, there was little evidence that broadcasting Great Horned Owl calls affected male Spotted Owl responsiveness at the temporal scale we evaluated for the experiment (M_T: $F_{1,9} = 0.22$, $P = 0.651$; M_{GHOW}: $F_{1,10} = 1.87$, $P = 0.201$). The means model was the top-ranked model based on AIC_C (Table 2). The second-best model was a treatment-only model, followed by a model with Great Horned Owl presence only. However, both of these

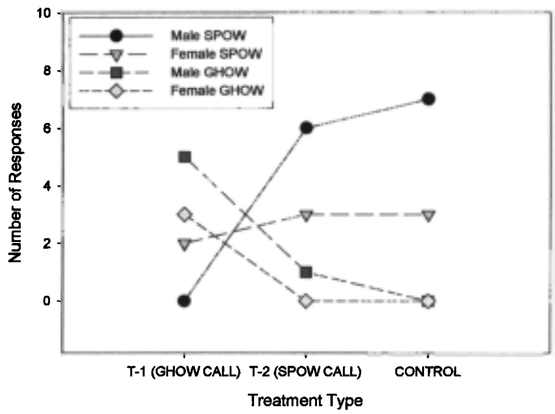

Figure 1. Number of owl responses following broadcast of Great Horned Owl calls (Treatment Day I = T1) and Spotted Owl calls (Treatment Day II = T2 and Control = CONTROL). Responses of both male and female Spotted Owls (SPOW) and Great Horned Owls (GHOW) were noted during all surveys. One Great Horned Owl detection where gender could not be determined was included as probable male.

models were >3 AIC_C units from the means model, indicating that support for these effects was weak. The specific estimates of fixed parameters for these latter models indicated that the slope estimates were not different from zero (Table 3). For the treatment-only model (M_T), the 90% confidence interval of the treatment estimate included zero ($\beta_T = 0.442 \pm 1.55$). The 90% confidence interval of the parameter estimate for the presence of a Great Horned Owl (M_{GHOW}) also included zero ($\beta_{GHOW} = -1.38 \pm 1.67$).

Table 2. Ranking of *a priori* models to assess the short-term responsiveness of male California Spotted Owls to simulated Great Horned Owl presence in the central Sierra Nevada, California. Ranking is based on AIC_C values; w_i values are Akaike weights.

MODEL	K[a]	LOG-LIKELIHOOD	AIC_C	ΔAIC_C	w_i[b]
$M_{(.)}$	2	243.2	91.1	0.0	0.725
M_T	3	43.3	94.1	3.0	0.162
M_{GHOW}	3	44.5	96.4	5.3	0.051
M_{T+P}	4	43.4	97.5	6.4	0.030
M_{T+C}	4	43.7	98.0	6.9	0.023
M_{T+GHOW}	4	44.8	100.2	9.1	0.008
M_{T*GHOW}	5	44.7	103.6	12.5	0.001

[a] K = number of parameters in model.
[b] w_i = Akaike weight = ($EXP^{-0.5 \times \Delta AIC_C}$ [specific model])/(Σ of ($EXP^{-0.5 \times \Delta AIC_C}$ [all models])).

DISCUSSION

We found no evidence that the simulated presence of Great Horned Owls had an effect on male Spotted Owl vocal responsiveness at the temporal scale of our evaluation. This suggests that conducting surveys for both species can be conducted on the same study area without biasing surveys for Spotted Owls given a reasonable lag (at least 24 hr) between surveys of each species. This result also weakens, but does not entirely refute (see below) the hypothesis that Spotted Owls select territories (habitat) to avoid Great Horned Owls (Carey 1985, Gutiérrez 1985). However, the low heterospecific response rates suggest that these species are not interspecifically territorial. Other studies of heterospecific and conspecific avian responsiveness have measured the response of one species to another species (Bosakowski and Smith 1998, Boal and Bibles 2001). Our study differed in one fundamental way from these studies because we broadcast calls of two species, a Great Horned Owl call followed, after a latent period, by a Spotted Owl call to assess whether the first species affected the response of the second species to conspecific calls. Given some level of background exposure (i.e., Spotted Owls may normally hear Great Horned Owls), conducting surveys of Great Horned Owls within Spotted Owl territories does not appear to alter detection of Spotted Owls or increase predation risk to Spotted Owls, at least at the temporal scale of our experiment. We noted that response to heterospecific calls by both species was low. This was consistent with other studies comparing responsiveness of raptor species to conspecific and Great Horned Owl calls (Johnson 1993, Bosakowski and Smith 1998, Boal and Bibles 2001). The low response rate to heterospecific calls and the high response rate of Spotted Owls to conspecific calls following exposure to Great Horned Owl calls also implies that Spotted Owls may not vocally defend their territories against Great Horned Owls, which we had expected to detect if interspecific competition was present. In addition, Spotted Owl response rates were very similar to response rates of Spotted Owls on a nearby study area, which suggested the experimental effect did not result in changes of the patterns of calling by Spotted Owls.

We did not measure immediate or long-term effects of broadcasting Great Horned Owl calls in

Table 3. Estimates of fixed parameters with associated standard errors, F, P-values, and degrees of freedom for hypothesized models explaining short-term responsiveness of male Spotted Owls to Spotted Owl calls after exposure to Great Horned Owl calls in the central Sierra Nevada, California. Models are presented according to rank based on AIC_C. For all parameters, estimates represent probability the Treatment (T) = control, Period (P) = 1st, Carryover (C) = no, and Great Horned Owl Present (GHOW) = no.

MODEL	PARAMETER	PARAMETER ESTIMATE (SE)	P-VALUE	F-VALUE[a]	df
$M_{()}$	μ	0.619 (0.469)	0.219		
M_T	μ	0.406 (0.646)			
	T	0.442 (0.945)	0.651	0.22	1, 9
M_{GHOW}		1.39 (0.791)	0.118		
	GHOW	−1.39 (1.01)	0.201	1.87	1, 10
M_{T+P}	μ	0.187 (0.791)	0.818		
	T	0.447 (0.949)	0.650	0.22	1, 8
	P	0.447 (0.949)	0.650	0.22	1, 8
M_{T+C}	μ	−0.575 (1.58)	0.724		
	T	0.990 (1.29)	0.469	0.58	1, 8
	C	0.990 (1.44)	0.516	0.46	1, 8
M_{T+GHOW}	μ	1.16 (0.906)	0.237		
	T	0.491 (1.00)	0.636	0.24	1, 9
	GHOW	−1.40 (1.03)	0.205	1.87	1, 9

[a] F-value calculated from Type III sums of squares.

Spotted Owl territories. Although we chose to be conservative when selecting an appropriate time interval, 24 hr may not have been the most appropriate stimulus-response interval to detect a difference in responsiveness (i.e., call suppression). If the primary goal of a study was to examine explicitly the behavioral interactions of the two species, we would recommend employing a shorter stimulus-response interval with appropriate consideration for increasing potential for predation of Spotted Owls. We also did not evaluate biological factors that might stimulate territorial defense such as brood defense. Although we did not assess reproduction of Spotted Owls in this study, Spotted Owl reproduction on the nearby EDSA was very low in 2003 (R.J. Gutiérrez unpubl. data), and reproduction is highly correlated among regional populations of Spotted Owls in the Sierra Nevada (Franklin et al. 2004). We are not certain what effect breeding status might have on Spotted Owl responsiveness.

Great Horned Owl detections within Spotted Owl territories were common following Great Horned Owl broadcasts. When Great Horned Owls were detected following the broadcast of Great Horned Owl calls (Treatment Day 1), 6 of 7 (85.7%) Great Horned Owls flew to within 50 m of the broadcast location and continued to call. Thus, surveying for Great Horned Owls caused movement of these predators into the survey area, which was within an occupied Spotted Owl territory; this validated some of our initial concern regarding risk to Spotted Owls. However, we noted no discernable effect on subsequent Spotted Owl vocal responsiveness after 24 hr. Because we detected Great Horned Owls in half of the Spotted Owl territories that we surveyed, it was likely that Spotted Owls were exposed regularly to Great Horned Owl calling. This might explain why we did not see a treatment effect. However, the model for Great Horned Owl presence was not a significant predicator of male Spotted Owl responsiveness. Thus, it appeared that neither artificial exposure nor live exposure to Great Horned Owls affected detection rates of Spotted Owls following our lag period.

Lack of vocal interaction between these two owl species suggests that (1) Great Horned and Spotted owls may not be strong competitors, (2) Great Horned Owls may prey on Spotted Owls only in an opportunistic manner, (3) these species segregate habitat on a fine scale even when apparently occupying the same general areas, or (4) some other mechanism has evolved to maintain ecological or spatial separation between these two species.

From a conservation perspective, it appears that Great Horned Owl surveys may not have a confounding effect on Spotted Owl population studies. Given the interest in the interspecific interactions of these owl species, our results suggest that surveying for Great Horned Owls would not affect the detection probability of Spotted Owls if surveys for the former species are conducted at least 24 hr apart from surveys of the latter species. Because Great Horned Owls occupy more open habitats and if their numbers increase in response to habitat fragmentation induced by logging, then the opportunity for Great Horned Owl predation on Spotted Owls may increase (Thomas et al. 1990). Such a numerical response might also suggest alternative silvicultural practices to reduce the impact of changing forest habitat that favors Great Horned Owls. Thus, Great Horned Owl surveys may be important to include in studies designed to monitor the effects of logging on Spotted Owl survival rates because timber removal may create more habitat suitable for this potential predator.

ACKNOWLEDGMENTS

We thank Foresthill, Georgetown, and Pacific U.S. Forest Service Ranger Districts and Forest Biologists Charis Parker, Matthew Triggs, and Don Yasuda for providing us with the location of historical Spotted Owl territories. We also thank our field technicians, J. Anfinson, B. Bloemke, A. Chatfield, M. Chatfield, J. Corcoran, S. Dallmann, and A. Rex for their assistance. Finally, we appreciate the thoughtful comments of E.D. Forsman and two anonymous reviewers. This study was funded by the U.S. Forest Service (contract FS53-91S8-00-EC14 to R. Gutiérrez) and the University of Minnesota.

LITERATURE CITED

AKAIKE, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267–281 *in* B.N. Petrov and F. Csaki [EDS.], Second international symposium on information theory. Akademiai Kiado, Budapest, Hungary.

BAUMGARTNER, F.M. 1939. Territory and population in the Great Horned Owl. *Auk* 56:274–282.

BOAL, C.W. AND B.D. BIBLES. 2001. Responsiveness of Elf Owls to conspecific and Great Horned Owl calls. *J. Field Ornithol.* 72:66–71.

BOSAKOWSKI, T. AND D.G. SMITH. 1998. Response of a forest raptor community to broadcasts of heterospecific and conspecific calls during the breeding season. *Can. Field-Nat.* 112:198–203.

BURNHAM, K.P. AND D.R. ANDERSON. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, NY U.S.A.

CAREY, A.B. 1985. The scientific basis for Spotted Owl management. Pages 110–114 *in* R.J. Gutiérrez and A.B. Carey [EDS.], Ecology and management of the Spotted Owl in the Pacific northwest. Gen. Tech. Rep. PNW-185, USDA, Forest Service Pacific Northwest Research Station, Portland, OR U.S.A.

FORSMAN, E.D. 1983. Methods and materials for locatıng and studying Spotted Owls in Oregon. Gen. Tech. Rep. PNW-162, USDA, Forest Service Pacific Northwest Research Station, Portland, OR U.S.A.

———, E.C. MESLOW, AND H.M. WRIGHT. 1984. Distribution and biology of the Spotted Owl in Oregon. *Wildl. Monogr.* 87:1–64.

———, R.G. ANTHONY, J.A. REID, P.J. LOSCHL, S.G. SOVERN, M. TAYLOR, B.L. BISWELL, A. ELLINGSON, E.C. MESLOW, G.S. MILLER, K.A. SWINDLE, J.A. THRAILKILL, F.F. WAGNER, AND D.E. SEAMAN. 2002. Natal and breeding dispersal of Northern Spotted Owls. *Wildl. Monogr* 149:1–35.

FRANKLIN, A.B., D.R. ANDERSON, E.D. FORSMAN, K.P. BURNHAM, AND F.W. WAGNER. 1996. Methods for collecting and analyzing demographic data on the Northern Spotted Owl. *Stud. Avian Biol.* 17:12–20.

———, R.J. GUTIÉRREZ, J.D. NICHOLS, M.E. SEAMANS, G C. WHITE, G.S. ZIMMERMAN, J.E. HINES, T.E. MUNTON, W.S. LAHAYE, J.A. BLAKESLEY, G.N. STEGER, B.R. NOON, D.W.H. SHAW, J.J. KEANE, T.L. MCDONALD, AND S. BRITTING. 2004. Population dynamics of the Californıa Spotted Owl (*Strix occidentalis occidentalis*): a meta-analysis. *Ornithol. Monogr.* 54.

GANEY, J.L., W.M. BLOCK, J.S. JENNESS, AND R.A. WILSON 1997. Comparative habitat use of sympatric Mexican Spotted and Great Horned owls. *J. Wildl. Res.* 2:115–123.

GUTIÉRREZ, R.J. 1985. An overview of recent research on the Spotted Owl. Pages 39–49 *in* R.J. Gutiérrez and A.B. Carey [EDS.], Ecology and management of the Spotted Owl in the Pacific northwest. Gen. Tech. Rep. PNW-185, USDA, Forest Service Pacific Northwest Research Station, Portland, OR U.S.A.

———, A.B. FRANKLIN, AND W.S. LAHAYE. 1995. Spotted Owl (*Strix occidentalis*). *In* A. Poole and F. Gill [EDS], The birds of North America, No. 179. The Birds of North America, Inc., Philadelphia, PA U.S.A.

HOUSTON, C.S., D.G. SMITH, AND C. ROHNER. 1998. Great Horned Owl (*Bubo virginianus*). *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 372. The Birds of North America, Inc., Philadelphia, PA U.S.A.

JOHNSON, D.H. 1993. Spotted Owls, Great Horned Owls, and forest fragmentation in the central Oregon Cascades. M.S. thesis, Oregon State Univ., Corvallis, OR U.S.A.

KÜCHLER, A.W. 1977. The map of natural vegetation of California. Pages 909–938 *in* M.G. Barbour and J. Major [EDS.], Terrestrial vegetation of California. J. Wiley and Sons, New York, NY U.S.A.

LITTELL, R.C., G.A. MILLIKEN, W.W. STROUP, AND R.D. WOLFINGER. 1996. SAS system for mixed models. SAS Institute, Cary, NC U.S.A.

MCGARIGAL, K. AND J.D. FRASER. 1984. The effect of forest stand age on owl distribution in southwestern Virginia. *J. Wildl. Manag.* 48:1393–1398.

MILLER, L. 1930. The territorial concept in the horned owls. *Condor* 32:290–291.

MILLER, G.S. AND E.C. MESLOW. 1985. Dispersal data for Spotted Owls: the problem of small sample size. Pages 69–73 *in* R.J. Gutiérrez and A.B. Carey [EDS.], Ecology and management of the Spotted Owl in the Pacific northwest. Gen. Tech. Rep. PNW-185, USDA, Forest Service Pacific Northwest Research Station, Portland, OR U.S.A.

MØLLER, A.P. 1992. Interspecific response to playback of bird song. *Ethology* 90:315–320.

MORRELL, T.E., R.H. YAHNER, AND W.L. HARKNESS. 1991. Factors affecting detection of Great Horned Owls by using broadcast vocalizations. *Wildl. Soc. Bull.* 19:481–488.

ORIANS, G.H. AND M.F. WILLSON. 1964. Interspecific territories of birds. *Ecology* 45:736–745.

PHILLIPS, A.R., J. MARSHALL, AND G. MONSON. 1964. The birds of Arizona. Univ. Arizona Press, Tucson, AZ U.S.A.

RATKOWSKI, D.A., M.A. EVANS, AND J.R. ALLDREDGE. 1993. Cross-over experiments: design, analysis, and application. Marcel Dekker, Inc., New York, NY U.S.A.

REID, J.A., R.B. HORN, AND E.D. FORSMAN. 1999. Detection rates of Spotted Owls based on acoustic-lure and live-lure surveys. *Wildl. Soc. Bull.* 27: 986–990.

RUDOLPH, S.G. 1978. Predation ecology of coexisting Great Horned and Barn owls. *Wilson Bull.* 90:134–137.

SAS INSTITUTE, INC. 2001. SAS software version 8.02 for Windows. SAS Institute, Inc., Cary, NC U.S.A.

SEAMANS, M.E., R.J. GUTIÉRREZ, C.A. MOEN, AND M.Z PEERY. 2001. Spotted Owl demography in the central Sierra Nevada. *J. Wildl. Manag.* 65:425–431.

SENN, S. 1993. Cross-over trials in clinical research. John Wiley and Sons, Ltd., New York, NY U.S.A.

STOKES, D., L. STOKES, AND K.J. COLVER. 1999. Stokes field guide to bird songs: western region. Time Warner Audiobooks, New York, NY U.S.A.

THOMAS, J.W., E.D. FORSMAN, J.B. LINT, E.C. MESLOW, B.R. NOON, AND J. VERNER. 1990. A conservation strategy for the northern Spotted Owl. Report of the Interagency Scientific Committee to address the conservation of the northern Spotted Owl. U.S. Department of Agriculture, Forest Service, U.S. Department of Interior, Bureau of Land Management, Fish and Wildlife Service, and National Park Service. U.S. Government Printing Office 791-171/20026, Washington, DC U.S.A.

USDA FOREST SERVICE. 1993. Protocol for surveying for Spotted Owls in proposed management activity areas and habitat conservation areas. Pacific Southwest Region, San Francisco, CA U.S.A.

USDI. 1990. Endangered and threatened wildlife and plants; determination of threatened status for the northern Spotted Owl. Federal Register 55:26114–26194, U.S. Department of Interior, Washington, DC U.S.A.

Received 17 March 2004; accepted 11 December 2004