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Response of Red-Cockaded Woodpeckers to Military Training Operations

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ABSTRACT Military lands are a valuable resource in recovery of threatened, endangered, and at-risk species worldwide and have the highest density of threatened and endangered species of all major land management agencies in the United States. Many red-cockaded woodpeckers (*Picoides borealis*) that reside on federal lands occur on 15 military installations in the southeastern United States. This close association has increased concern over potential conflicts between conservation requirements of endangered species and the military's mission of combat readiness. Our objectives were to 1) determine if military training operations affect behavior, reproductive success, and productivity of red-cockaded woodpeckers; 2) develop a frequency-weighting function to assess woodpecker hearing sensitivity; 3) identify factors that affect woodpecker responses to military training operations; 4) develop distance and dose-response thresholds for quantifying woodpecker responses to noise levels and stimulus distances; 5) characterize military training operations through quantification of sound levels, source identification, distance from active woodpecker nests, frequency spectra, duration, and frequency of occurrence; and 6) document baseline woodpecker nesting behavior. We conducted our study on the Fort Stewart Military Installation located in southeast Georgia, USA.

Downy woodpeckers, as surrogates for red-cockaded woodpeckers, had their best hearing sensitivity within the peak range of the power spectrum of both downy and red-cockaded woodpecker vocalizations, which is at a higher frequency than that of a typical passerine. Overall, woodpeckers had a reduced auditory sensitivity relative to human hearing sensitivity and other species of small birds, especially in the frequency range >4 kHz. Woodpeckers were most sensitive in the 1.5- to 4.0-kHz range. Sensitivity appeared to drop off quickly at frequencies <1.0 kHz and >4.0 kHz. Overall, we did not find that the woodpecker-frequency-weighting function we developed provided a better predictor of woodpecker flush response compared with A-weighting. More research is needed to better understand the relationship between frequency-weighting functions and woodpecker response behavior.

Potential breeding groups of woodpeckers across the population increased from 158 in 1997 to 181 in 2000, wheras nesting groups increased from 141 in 1998 to 170 in 2000, for overall increases of 14.6% and 20.6%, respectively, over the 3 years of this project. Fledging success rates for individual nests within the overall population remained consistent from 1998 to 2000, averaging 84.4%. Mean clutch sizes for woodpecker groups for 1998 to 2000 ranged from 2.75 to 3.01 eggs/nest, brood size ranged from 2.01 to 2.22 nestlings/nest, whereas the average number of young fledged ranged from 1.57 to 1.76 young/occupied nest. We observed no difference in reproductive success or productivity between experimental and control-tested red-cockaded woodpecker groups. Overall, experimental test groups produced an average of 2.98 eggs/nest, 1.89 nestlings/nest, and 1.54 young/occupied nest from 1999 to 2000, compared with 2.73 eggs/nest, 1.91 nestlings/nest, and 1.57 young/occupied nest at control groups.

We measured behavioral responses (nest attendance and arrivals and departures from the nest) of red-cockaded woodpeckers to military training events through direct and indirect (i.e., video surveillance) observation of 464.5 hours of woodpecker nesting behavior before and after controlled experimental events while recording and characterizing military-generated sound events using sound-recording equipment. We presented woodpeckers with actual 0.50-caliber blank machine gun fire and artillery simulators from controlled distances to develop distance and sound thresholds. We used video surveillance to document potential behavioral responses of woodpeckers primarily during nonexperimental military training operations in areas that could not be safely monitored and to determine baseline woodpecker nesting behaviors. We recorded 2,846 nonexperimental military noise events in 157 data sessions at 50 red-cockaded woodpecker groups from 1998 to 2000. We also recorded 206 experimental tests at 58 woodpecker groups during 1999 and 2000.

Life-table analyses of flush response time showed that at short ranges (15–30 m) the flush response was stronger for artillery simulator blasts than for blank fire in both the incubation and the nestling phases. In contrast, at medium distances (45–60 m) blank fire tended to produce more flush responses than artillery fire in both incubation and nestling phases. At longer distances (>60 m), blank fire and artillery produced similar flush responses in the incubation phase, whereas flush response was stronger for blank fire than for artillery in the nestling phase. In general, most animals that responded to military activity flushed within 5 seconds of the stimulus event. Woodpeckers returned to nests within an average of 4.4 minutes after being flushed by artillery simulators and 6.3 minutes after 0.50-caliber blank-fire tests. Woodpecker flush response rates increased as stimulus distance decreased and sound levels increased, regardless of stimulus type or year. Woodpeckers did not flush from nests when 0.50-caliber blank machine gun fire and artillery simulators were >152 m away and sound-exposure levels (decibels [dB]) were <68 dBW (woodpecker-based frequency-weighting curve) and <65 dBW, respectively.

We found that blast treatments reduced arrival rates of adults at the nest, with the amount of reduction dependent on the type of blast stimulus and number of helpers at the nest. On the other hand, blast treatments had no detectable effects on nest attendance. The effect of blank fire on incubation-phase arrivals over a 30-minute interval (about 40% reduction) was nearly twice that of artillery simulator fire (about a 20% reduction). There was no evidence supporting any effect of stimulus type on arrivals during the nestling phase. Blast stimuli during incubation reduced arrivals by 40% when no helpers were present, but the strength of this effect decreased to 28% when one helper was present, and was only 6% for nests with ≥2 helpers. Distance of the blast from the nest did not affect the response of arrival rates to blast treatments.

Infrequent, short-duration military training exercises, as measured, did not appear to substantially impact red-cockaded woodpecker reproductive success and productivity on the Fort Stewart Military Installation. Our results may be applicable to other military installations where similar training activities and intensity levels occur. Additional research is needed to address possible habituation or sensitization of red-cockaded woodpeckers to human activities in proximity to active nest sites. Although we attempted to monitor woodpecker response to a number of military training activities, other types of military training operations or human-based activities with louder noise, longer duration, increased human presence, and greater frequency of occurrence could more negatively influence woodpecker nesting behavior and need to be investigated. Our results do not support the hypothesis that military

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maneuver training operations are limiting factors in the recovery of red-cockaded woodpeckers on military installations, based on our level and type of testing. Natural resource management policies on military installations have had a positive influence on the recovery of red-cockaded woodpeckers and probably outweigh the negative effects of typical military training. © 2011 The Wildlife Society.

KEY WORDS behavioral response, flush, Fort Stewart, Georgia, military training, noise disturbance, *Picoides borealis*, red-cockaded woodpecker, sound recording, video surveillance, woodpecker weighting curve.

Respuesta del Pájaro Carpintero de Cresta Roja a las Operaciones del Entrenamiento Militar

RESUMEN Las tierras militares son recursos valerosos en el recobro de los especies amenazados, en peligro de extinción, y arriesgados, y tienen la densidad mas alta de especies amenazados y en peligro de extinción por hectárea de todas las mayores agencias de gestión de tierras en EEUU. Un gran porcentaje de los pájaros carpinteros de cresta roja (*Picoides borealis*) que residen en tierras federales, ocurren en quince instalaciones militares en el suroeste de EEUU. Tal estrecha asociación ha incrementado preocupaciones con los conflictos potenciales entre los requerimientos de conservación de especies en peligro de extinción y la misión militar de mantener la preparación para combate. El objetivo de esta investigación fue para 1) determinar si las operaciones de entrenamiento militar afectan a la conducta y capacidad de reproducción de los pájaros carpinteros de cresta roja; 2) desarrollar una función de carga de frecuencia para estimar la sensibilidad del oído de los datos de repuesta del tronco cerebral auditorio del los pájaros carpinteros peludos como especie substituto por los pájaros carpinteros de cresta roja; 3) identificar los factores que afectan las respuestas de los pájaros carpinteros a las operaciones del entrenamiento militar; 4) desarrollar umbrales de distancia y de respuesta de dosis para cuantificar las respuestas de los pájaros carpinteros a los niveles de ruidos y a las distancias de los estímulos; 5) caracterizar las operaciones de entrenamiento militar por la cuantificación de las niveles de sonido, identificación del origen, la distancia de los nidos activos de los pajaraos carpinteros, espectros de frecuencia, duración, y frecuencia de ocurrencia; y 6) documentar el base del la conducta de anidar de los pájaros carpinteros. Conducimos estas investigaciones en Fort Stewart, localizados en el suroeste del estado de Georgia, EEUU. Los pájaros carpinteros peludos, como sustitutos por los pájaros carpinteros de cresta roja, exhibieron su mejor sensibilidad del oído dentro del máximo rango del espectro de poder de ambos vocalizaciones de los pájaros carpinteros y los pájaros peludos, cual es en una frecuencia mas alta que la paseriformes típicas. En general, los pájaros carpinteros tenían una sensibilidad auditoria reducida en relación a la sensibilidad auditoria humana y a los otros especies de pájaros pequeños, especialmente in el rango mas alto de 4 kHz. Los pájaros carpinteros eran los mas sensibles en el rango de 1.5–4.0 kHz. La sensibilidad pareció caerse rápidamente a las frecuencias debajo de 1.0 kHz y mas que 4.0 kHz. En general, no encontramos que la función de carga de frecuencia de los pájaros carpinteros que fue desarrollado como parte de este proyecto proveyó un mejor predictor de la respuesta de los pájaros carpinteros levantar de pieza comparado con una curva de ponderación A. Hay necesidad de mas investigaciones para entender mejor la relación entre funciones de ponderación de frecuencia y la respuesta de comportamiento de los pájaros carpinteros.

Medimos las reacciones de comportamiento (nido de asistencia, y llegadas y salidas del nido) de los pájaros carpinteros de cresta roja a los eventos de entrenamiento militar por observación directa y indirecta (es decir, video vigilancia), observación de 464.5 horas de la conducta de anidar de los pájaros carpinteros antes y después del los eventos experimentales controlados, mientras que simultáneamente grabamos y caracterizamos los eventos de ruidos originados por el militar con equipo de grabar. Los pájaros carpinteros fueron enfrentados con fuego en blanco de ametralladora de calibre 0.50 o de simuladores de artillería de distancias controladas para desarrollar los umbrales de distancia y sonido. La vigilancia video fue utilizado para documentar la reacción potencial de comportamiento de los pájaros carpinteros primariamente durante operaciones del entrenamiento militar no experimental en los áreas en que no se pudiera monitorizar sin peligroy para determinar un base del la conducta de anidar de los pájaros carpinteros. Grabamos 2,846 eventos no experimentales de ruidos militares durante 157 sesiones con 50 grupos de los pájaros carpinteros de cresta roja del año 1998 por 2000. También grabamos 206 pruebas experimentales con 58 grupos de los pájaros carpinteros de cresta roja durante 1999–2000. Análisis de tabla-vida de la respuesta de los pájaros carpinteros levantar de pieza enseñan que a corta distancia (15–30 m), la respuesta de levantar era mas fuerte para simulador de explosiones de artillería que para fuego en blanco en ambos fases de incubación y de cría. En contraste, a las distancias medianas (45–60 m), el fuego en blanco tenia la tendencia a producir mas respuestas de levantar que fuego de artillería en ambos fases de incubación y de cría. A las distancias mas largas (>60 m), el fuego en blanco y de artillería produjeron respuestas de levantar similares en el fase de incubación, mientras que la respuesta de levantar era mas fuerte para fuego en blanco que para artillería en el fase de cría. En general, la mayor parte de los animales que respondieron a la actividad militar se levantaron dentro 5 secundas del evento de estímulo. Los pájaros carpinteros regresaron a los nidos dentro 4.4 minutos, por término medio, después de haber estado levantado de pieza por los simuladores de artillería, y 6.3 minutos después de pruebas con fuego en blanco de de ametralladora de calibre 0.50. La tasa de respuesta de los pájaros carpinteros levantar de pieza se aumentó cuando se disminuyó la distancia del estimulo y cuando se aumentó los niveles do los sonidos, a pesar del tipo del estimulo o del año. Los pájaros carpinteros no se levantaron de la pieza cuando fuego en blanco de ametralladora de calibre 0.50 y simuladores de artillería estaban >152 m de distancia y los niveles de exposición a sonidos estaban <68 dBW (ponderación de frecuencia basada en pájaros carpinteros) y 65 dBW, respectivamente.

Encontramos que los tratamientos de explosiones redujeron la tasa de los llegados de adultos a los nidos en esta investigación, y la cantidad de reducción dependía en el tipo de estimulo de fuego y el numero de los ayudantes a los nidos. Por otra parte, los tratamientos de fuego no tenían efectos detectables en asistencia en los nidos es esta investigación. El efecto del fuego en blanco en llegados durante el fase de incubación por un intervalo de 30 minutos (una reducción acerca de 40%) era casi doble lo del fuego de artillería (acerca de 20%). No habia evidencia que soportaba que cualquier tipo del estimulo afectaba llegados durante el fase de cría. Los estímulos durante incubación redujeron llegados por 40% cuando no estaban ayudantes, pero la fuerza de este efecto se disminuyó a 28% cuando estaba un ayudante, y era 6% para nidos con dos o mas ayudantes. La distancia de la explosión del nido no afectaba la respuesta de la tasa de llegados a los tratamientos del las explosiones en esta investigación.

Los pájaros carpinteros peludos, como sustitutos por los pájaros carpinteros de cresta roja, exhibieron su mejor sensibilidad del oído dentro del máximo rango del espectro de poder de ambos vocalizaciones de los pájaros carpinteros y los pájaros peludos, cual es en una frecuencia mas alta que la paseriformes típicas. En general, los pájaros carpinteros tenían una sensibilidad auditoria reducida en relación a la sensibilidad auditoria humana y a los otros especies de pájaros pequeños, especialmente in el rango mas alto de 4 kHz. Los pájaros carpinteros eran los mas sensibles en el rango de 1.5-4.0 kHz. La sensibilidad pareció caerse rápidamente a las frecuencias debajo de 1.0 kHz y mas que 4.0 kHz. En general, no encontramos que la función de carga de frecuencia de los pájaros carpinteros que fue desarrollado como parte de este proyecto proveyó un mejor predictor de la respuesta de los pájaros carpinteros levantar de pieza comparado con una curva de ponderación A. Hay necesidad de mas investigaciones para entender mejor la relación entre funciones de ponderación de frecuencia y la respuesta de comportamiento de los pájaros carpinteros.

Ejercicios militares infrecuentes, y de corta duración, como medidos, no aparecían a impactar significativamente al éxito reproductivo y productividad de los pájaros carpinteros de cresta roja en la instalación militar de Fort Stewart. Estos resultados podría ser aplicable a otras instalaciones militares donde ocurren actividades de entrenamiento y de niveles de intensidad similares. Hay necesidad de mas investigaciones para abordar la posible habitación o sensibilización de los pajaraos carpinteros de cresta roja a las actividades humanas en la proximidad de sitios de nidos activos. Aunque tratamos a monitorizar las respuestas de los

pájaros carpinteros a varios actividades de entrenamiento militar, otros tipos de operaciones de entrenamiento militar o actividades humanos mas bulliciosos y prolongados, y con aun mas presencia humana, podría influir la conducta de anidar de los pájaros carpinteros, y debe ser investigados. Nuestros resultados no soportan el hipótesis que las maniobras de formación son factores limitantes en el recobro de los pájaros carpinteros de cresta roja en las instalaciones militares basados en el nivel y tipo de las pruebas. Las políticas de administración de los recursos naturales en las instalaciones militares han tenido una influencia positiva en el recobro del pájaro carpintero de cresta roja y probablemente superan los efectos negativos del entrenamiento militar que esta llevando a cabo.

La Reponse des Pics à Face Blanche aux Exercices d'Entraînement Militaire

RÉSUMÉ Les terrains appartenant aux services militaires constituent une ressource de haute valeur dans la récupération des espèces vulnérables, menacées et en voie de disparition à travers le monde. Aux Etats-Unis, ces terrains possèdent la densité par hectare la plus importante des espèces menacées et en voie de disparition de tous les bureaux fonciers notables. Une grande proportion de pics à face blanche (*Picoides borealis*) résidant sur les terrains du gouvernement fédéral occupe une quinzaine d'installations militaires dans le sud-est des États-Unis. Cette proximité a généré de la discorde entre l'obligation de conserver les espèces en voie de disparition et le but militaire de la préparation au combat. Les buts de l'étude ici présentée étaient de 1) déterminer si les exercices d'entraînement militaire ont une influence sur le comportement et la santé reproductrice du pic à face blanche, 2) développer une courbe de déformation de la fréquence destinée à estimer la sensitivité auditive du pic selon la réponse auditive du tronc cérébral (*auditory brainstem response* [ABR]) du pic mineur, étant une espèce succédanée des pics à face blanche, 3) identifier les facteurs agissant sur les réponses du pic aux exercices d'entraînement militaire, 4) développer des seuils de distance et de dose-réponse afin de quantifier la réaction du pic à face blanche aux bruits et aux différentes distances des stimuli, 5) caractériser les exercices d'entraînement militaire à travers une quantification de leurs propriétés sonores, leurs sources, leur spectre d'énergie acoustique, leur durée, leur fréquence, et 6) établir le comportement de nidification basique du pic à face blanche. Cette étude a été entreprise à Fort Stewart, dans le sud-est de la Georgie aux USA. Il a été établi que la meilleure sensibilité auditive des pics mineurs, comme espèce succédanée pour les pics à face blanche, se trouve à l'intérieur du points maximaux du spectre d'énergie des vocalisations du pic mineur et du pic à face blanche, ce qui se place à une plus haute fréquence que celle d'une passerine typique. Globalement, les pics possèdent une sensibilité auditive réduite par rapport aux êtres humains et les autres espèces de petits oiseaux, surtout dans les hautes fréquences. Les pics se sont montrés le plus sensible aux bruits dans la plage de 1,5 à 4,0 kHz. Cette sensibilité semblait diminuer brusquement aux fréquences en dessous de 1,0 kHz et celles supérieures à 4,0 kHz. Dans l'ensemble, nous n'avons pas trouvé que la fonction de déformation de la fréquence des pics élaborée comme partie de ce projet de recherches donne de meilleures prédictions de réponses de dénidification des pics que celles générées par *A-weighting.* Davantage de recherches sont nécessaire pour mieux comprendre la relation entre les fonctions de déformation de fréquence et le comportement de réponse du pic.

Nous avons mesuré les réponses du pic à face blanche (la présence au nid aussi bien que les arrivées et les départs du nid) aux vrais incidents d'entraînement militaire à travers l'observation directe et indirecte (la vidéosurveillance) de 464.5 heures de comportement de nidification du pic pendant que l'on enregistrait et catégorisait les évènements sonores issus des exercices militaires avec des équipements d'enregistrement acoustique. Les pics ont été mis en présence de vraie fusillade de mitrailleuse à calibre 0,50 et des simulateurs d'artillerie à des distances contrôlées afin de pouvoir mesurer les seuils de distance et de son. La vidéosurveillance a été employée pour enregistrer la réponse du pic aux entraînements militaires passifs dans les endroits où l'observation directe auraient été hasardeuse et pour déterminer la ligne de fond des comportements de nidification du pic. Nous avons enregistré 2.846 évènements passifs de bruit militaire lors de 157 séances de collecte de données auprès de 50 groupes de pics à face blanche de 1998 à 2000. Nous avons également enregistré 206 tests expérimentaux auprès de 58 groups de pics de 1999 à 2000.

Des analyses de survie (*life-table analysis*) de la réponse du délai de nidification a montré que, à de petites distances (15–30 m), la réponse de nidification était plus forte pour les simulateurs d'artillerie que pour le feu des cartouches à blanc dans la phase d'incubation et d'oisillon. Pour les distances moyennes (45–60 m), en revanche, le feu des cartouches à blanc avait tendance à augmenter plus la réponse de nidification par rapport au feu d'artillerie pour dans les phases d'incubation et d'oisillon. Aux longues distances (>60 m), le feu des cartouches à blanc et les simulateurs d'artillerie ont produit des réponses de nidification comparables dans la phase d'incubation, tandis que cette réponse a été plus forte pour le feu des cartouches à blanc que pour les simulateurs d'artillerie pendant la phase d'oisillon. En général, la plupart des animaux ont quitté leur nid dans les 5 secondes qui suivaient le commencement du stimuli. Les pics ont repris leurs nids dans les 4,4 minutes suivant leur dénidification par les simulateurs d'artillerie et 6,3 minutes après les tests entrepris avec le feu des cartouches à blanc de calibre 0,50. Les taux de réponse de dénidification du pic ont augmenté au fur et à mesure que la distance du stimuli a été atténuée et les niveaux sonores ont été haussés, malgré le type de stimuli et l'année. Les pics n'ont pas déniché lorsque le feu des cartouches à blanc de calibre 0.50 et les simulateurs d'artillerie ont été placés à des distances supérieures à 152 m et quand les niveaux de contact sonore étaient <68 dBW (selon la courbe de déformation de la fréquence du pic) et <65 dBW, respectivement.

Nous avons établi que les traitements d'explosion ont réduit les taux d'arrivées des adultes au nid, une réduction dépendante du type de stimuli d'explosion et le nombre d'assistants auxiliaires (les jeunes pics aidant dans le processus d'élever les nouveaux-nés) présents au nid. D'un autre côté, nous n'avons trouvé aucun effet des traitements d'explosion sur la présence au nid. L'effet du feu des cartouches à blanc sur les arrivées pendant la période d'incubation à travers des intervalles de 30 minutes (une réduction d'environ 40%) a été le double de celui de la vraie fusillade (réduction d'environ 20%). Il n'y a pas eu d'évidence soutenant un effet quelconque du type de stimuli sur les arrivées lors de la phase d'oisillon. Les stimuli d'explosion pendant l'incubation ont fait baissé les arrivées par 40% quand aucun assistant auxiliaire n'était présent, mais l'importance de cet effet descend à 28% quand un seul assistant était présent et n'était que 6% pour les nids équipés de deux assistants ou plus. La distance entre l'explosion et le nid n'a pas eu d'effet sur la réponse des taux d'arrivées aux traitements d'explosion dans cette étude.

Il a été établi que la meilleure sensibilité auditive des pics mineurs, comme espèce succédanée pour les pics à face blanche, se trouve à l'intérieur du points maximaux du spectre d'énergie des vocalisations du pic mineur et du pic à face blanche, ce qui se place à une plus haute fréquence que celle d'une passerine typique. Globalement, les pics possèdent une sensibilité auditive réduite par rapport aux êtres humains et les autres espèces de petits oiseaux, surtout dans les hautes fréquences. Les pics se sont montrés le plus sensible aux bruits dans la plage de 1,5 à 4,0 kHz. Cette sensibilité semblait diminuer brusquement aux fréquences en dessous de 1,0 kHz et celles supérieures à 4,0 kHz. Dans l'ensemble, nous n'avons pas trouvé que la fonction de déformation de la fréquence des pics élaborée comme partie de ce projet de recherches donne de meilleures prédictions de réponses de dénidification des pics que celles générées par « A-weighting ». Davantage de recherches sont nécessaire pour mieux comprendre la relation entre les fonctions de déformation de fréquence et le comportement de réponse du pic.

Les exercices d'entraînement militaire peu fréquents, comme ceux mesurés ici, ne bouleversent pas particulièrement les paramètres de santé reproductrice du pic à face blanche au Fort Stewart Military Installation. Ces résultats pourraient être applicables à d'autres installations militaires où ont lieu des exercices des niveaux d'entraînement et d'intensité comparables. De plus amples recherches doivent être entreprises sur l'habituation

possible ou la sensibilisation des pics à face blanche aux activités humaines en proximité aux sites actifs de nidification. Même si l'on a tenté d'observer la réponse du pic aux différentes activités d'entraînement militaire, d'autres types d'opérations d'entraînement militaire ou d'activités humaines de durée plus longue ou comportant d'avantage de présence humaine et une manifestation plus fréquente, pourraient engendrer un impact négatif sur la nidification du pic et devraient être étudiés. Ces résultats ne soutiennent nullement l'hypothèse selon laquelle les opérations d'entraînements militaires constituent des facteurs limitants dans la rétablissement des pics à face blanche sur les installations militaires selon nos niveaux et nos méthodes. Jusqu'à présent, les politiques de gestion des ressources naturelles sur les installations militaires ont eu une influence positive sur le rétablissement des pics à face blanche et elles doivent probablement l'emporter largement sur les inconvénients de l'entraînement militaire tel qu'il est actuellement entrepris.

Contents

INTRODUCTION

Red-cockaded woodpeckers (*Picoides borealis*) inhabit mature, open pine forests of the southeastern United States (Jackson 1994). These woodpeckers are unusual among birds for their cooperative breeding system (Walters 1991, Jackson 1994), where young helpers, mostly male, from previous nests forego breeding to assist in raising the young of their parents or other kin (Ligon 1970, Lennartz et al. 1987, Walters et al. 1988, Haig et al. 1994). These helpers participate in all aspects of nesting, from incubation to brooding and feeding of nestlings to territorial defense for up to 8 years, although most breed themselves within a few years (Walters et al. 1988, U.S. Fish and Wildlife Service [USFWS] 2003). The life history tactics of cooperative breeding and a proclivity to re-nest after nest failure strongly affect population dynamics of this species. These tactics also may act as a buffer in regulating woodpecker populations due to mortality and productivity and could possibly lessen effects from other potential human-based disturbances (Walters 1991, Walters et al. 1992, 2002; USFWS 2003).

Home-range size, group size, and group reproductive measures may vary among woodpecker populations based on quality of the foraging habitat (DeLotelle and Epting 1992, USFWS 2003). This apparent inverse relationship between quantity and quality of foraging habitat strongly suggests the need to maintain and restore quality foraging habitat to sustain red-cockaded woodpecker populations (USFWS 2003). An important limited resource associated with territory quality is presence of available cavities for roosting and nesting, especially in areas with suboptimal habitat quality (Spadgenske 2002, USFWS 2003, Spadgenske et al. 2005). Upwards of 27 species of vertebrates are known to use cavities excavated by red-cockaded woodpeckers, which can lead to intense competition for woodpecker cavities, as is evident when artificial cavities are quickly claimed when provisioned in suitable but unoccupied habitat for red-cockaded woodpeckers (Jackson 1978, Harlow and Lennartz 1983, Rudolph et al. 1990*a*, Kappes and Harris 1995, Walters et al. 1992).

The red-cockaded woodpecker was listed as endangered throughout its range on 13 October 1970 and received federal protection under the Endangered Species Act through its passage in 1973. Habitat loss has been cited as the most important factor leading to decline of these woodpeckers throughout their range (USFWS 2003). Intensive logging for lumber and clearing of

forests for agriculture are leading causes of habitat loss (Frost 1993, Martin and Boyce 1993). Human-based activities, such as fire suppression and clear cutting, further compromise the integrity of longleaf pine ecosystems and associated red-cockaded woodpecker populations (Landers et al. 1995). Consequently, red-cockaded woodpecker populations have experienced severe reductions in the number of available cavity trees and have become fragmented in distribution (Costa and Escano 1989, Rudolph et al. 1990*a*, Conner et al. 1991, USFWS 2003).

Department of Defense and Red-Cockaded Woodpeckers

Department of Defense (DoD) lands are a valuable resource in the recovery of threatened, endangered, and at-risk species worldwide. Department of Defense lands have the highest density of threatened and endangered species of all major land management agencies in the United States (Flather et al. 1994). Historically, red-cockaded woodpeckers were widely distributed throughout the southern United States from eastern Texas to the Atlantic coast, and north to New Jersey (Jackson 1987). Distribution has been reduced with the extirpation of red-cockaded woodpeckers from New Jersey (Lawrence 1867), Missouri (Cunningham 1946), Maryland (Devlin et al. 1980), and most recently Kentucky (Mills et al. 2005). Most red-cockaded woodpeckers are currently restricted to public lands (national forests, military installations, and wildlife refuges). Nearly 35% of active red-cockaded woodpecker groups on federal lands occur on 15 military installations in the southeastern United States (USFWS 2003). This close association between red-cockaded woodpeckers and the DoD has led to increased concern over potential conflicts between endangered species conservation requirements and the military's mission of maintaining combat readiness (Delaney 2002). There are concerns that military training capability will erode if research is not initiated to investigate potential effects of military-unique operations, such as weapons noise (Jackson 1983, Doresky et al. 2001), maneuvers (J. Mobley, University of Central Arkansas, unpublished report; Hayden et al. 2002; Perkins 2006), and fog-oil-smoke obscurants (Smith et al. 2005) on red-cockaded woodpeckers.

The United States Army initially established a precautionary 61-m buffer zone in 1984 around all red-cockaded woodpecker clusters, which included all trees a woodpecker group would use in a year, to protect nesting habitat from possible training impact, although no direct link between military training operations and impacts to red-cockaded woodpeckers had been established. At that time, training within clusters was limited to transient (i.e., <2 hr in duration) dismounted training. The buffer zone substantially restricted the amount of land available for field training exercises on Army lands, especially transient vehicle traffic (e.g., tank and infantry fighting vehicles) through woodpecker clusters. Field training exercises are important because they offer military units the ability to maintain training proficiency under realistic combat conditions (Hayden 1997*a*,*b*).

The Army issued revised guidelines in 1996 for the management of red-cockaded woodpeckers on military lands to reduce training restrictions and increase adaptive management of woodpecker habitat. Under the revised guidelines, certain transient military operations would be permitted as close as 15.2 m to individual woodpecker cavity trees within a cluster (Hayden 1997*a*,*b*). This reduction from a 61-m buffer zone (around all trees within a cluster) to 15.2 m (around individual trees within a cluster) substantially reduced the amount of land the Army was restricted from using within woodpecker clusters. It was estimated that Fort Bragg would realize a 60% increase in lands available for training, compared to 10% to 20% on Fort Stewart and 27% on Fort Benning (Hayden 1997*a*,*b*). These figures are probably conservative, considering that woodpecker densities have increased at all of these installations since the 1990s (Costa 2005). The Army was still restricted from conducting several training activities within 15.2 m of active woodpecker nest cavities: 1) military vehicle and personnel travel, including armor; 2) 0.50-caliber blank machine gun fire and 7.62-mm and below blank fire; 3) artillery and hand grenade simulators and other similar devices; 4) hand digging of hasty individual fighting positions; 5) use of smoke grenades and star cluster and parachute flares; and 6) smoke and haze operation. Additionally, no felling of trees was allowed within 800 m of cavity trees without permission, and all training was limited during the woodpecker's breeding season (Hayden 1997*a*,*b*). These restrictions prohibited tactical training to doctrinal standards.

A 1996 USFWS Biological Opinion required the Army to assess the effects of implementing the 1996 Army guidelines. Fort Stewart prepared a multispecies endangered species management plan for the installation (Endangered Species Management Planning Team [ESMPT], Ft. Stewart, Multi-species endangered species management plan, 2001) that described changes under these revised guidelines: 1) consideration will be given jointly to training mission requirements and red-cockaded woodpecker biological requirements when implementing the plan; 2) there will be a reduction in off-limit area for through-cluster maneuver traffic around cluster trees from 61 m to 15.2 m; 3) the types of training operations allowed within clusters will be expanded; 4) proactive management will be undertaken to achieve woodpecker population goals through recruitment cluster establishment and single group augmentation; 5) increased monitoring and reporting requirements will be upheld; 6) reductions in potential training restrictions will be implemented, giving base commanders less basis for objection to expanding woodpecker populations; and 7) provisions will be provided for critical mission areas that have no training restrictions on new clusters (ESMPT 2001).

The USFWS established a minimum number of active clusters required to maintain a viable population of red-cockaded woodpeckers on Fort Stewart, which the USFWS referred to as the installation regional recovery goal (IRRG; Beaty et al. 2005). The goal of red-cockaded woodpecker management on Fort Stewart is to meet the IRRG while eliminating conflicts with the training mission by eliminating the need for training restrictions (ESMPT 2001). The IRRG (or 500, whichever was less) was determined by dividing the total number of suitable and potentially suitable acres of red-cockaded woodpecker habitat by the average home-range size of woodpeckers in the region (1 cluster = 81 ha; Epting et al. 1995, Beaty et al. 2005). In addition to the Fort Stewart IRRG, there was also a mission-critical goal (411 active clusters), which was calculated as the area for mission-critical areas (i.e., areas where it was unacceptable for the military to have additional restrictions) divided by 81 hectares, minus the IRRG. This total number of protected clusters was considered to be compatible with the current military mission on Fort Stewart (ESMPT 2001). To meet the

USFWS goal of 500 potential breeding groups, the ESMPT (2001) proposed the establishment of additional supplemental recruitment clusters (SRCs). Supplemental recruitment clusters are woodpecker clusters on the installation that are not subject to standard USFWS requirements for woodpecker foraging habitat or training restrictions. Installation use of SRCs will not constrain future facilities development on Fort Stewart that supports training and nontraining capabilities (ESTPT 2001).

Hearing Sensitivity and Adaptation

Hearing has traditionally been defined as an animal's behavioral response to sound. A variety of methods have been used to study animal hearing from physiological, anatomical, and behavioral approaches. Birds are known to have a restricted hearing range between a few hundred Hz and about 10 kHz, which is similar to levels reported for humans and other mammals (Dooling 1980, 1982, 1992). Birds are believed to hear best in the range of 1 to 5 kHz, and on average, their vocalizations range from 0.5 to 6.0 kHz. Hearing sensitivity of birds at high frequencies correlates with the highest frequency contained within the species' vocalizations (Dooling 1980, 1982). Some birds have been found to be sensitive to frequencies outside the typical range for birds, such as the low-frequency sensitivity of the common pigeon (*Columba livia;* Quine 1978), or have greater absolute auditory sensitivity than typical birds (e.g, owls; Konishi 1973, Van Dijk 1973). Previous animal disturbance studies have assumed that A-weighting frequency functions (i.e., filters sound energy according to human hearing range and sensitivity at moderate sound levels; American National Standards Institute [ANSI] 2001*a*) provide an accurate estimate of how animals perceive sounds within their environment. Few studies have developed animal-specific frequency-weighting functions to estimate animal hearing sensitivity (Delaney et al. 1999), whereas no studies have tested frequency-weighting functions against empirical data.

Techniques using auditory brainstem responses (ABRs) have been employed for many years (Jewett 1970, Dooling et al. 2000) and are a proven method for studying sensitivity and functionality of animal auditory systems (Brittan-Powell et al. 2002, 2005; Krausman et al. 2004). Auditory brainstem responses are electrical potentials measured as voltage differences between electrodes placed on an animal's head during testing. Techniques using ABRs measure an animal's brain-wave response to an auditory stimulus as a series of peaks and troughs generated by discharge of neurons in the brainstem (Fig. 1). Auditory brainstem response measures are frequently used to test avian species, provide precise peak latencies with low variability, can generate results quickly, and are not thought to be negatively impacted in most cases by anesthetics, which are commonly used to restrain animals during testing (Corwin et al. 1982, Smith and Mills 1989, Brittan-Powell et al. 2002, Lucas et al. 2002, Krausman et al. 2004, Brittan-Powell et al. 2005). It is important to note that although they are accurate predictors of audiogram shape (which is of primary importance for a frequency-weighting filter), ABR techniques may not completely represent the auditory sensitivity pattern of an animal, particularly as regards actual hearing sensitivity (Brittan-Powell et al. 2002).

Adaptations to dampen mechanical shock during pecking could play a role in shaping hearing abilities of woodpeckers. These species experience extreme impact-deceleration exposure during daily activities involving foraging, cavity construction, and resin-well maintenance. The unique cranial anatomy and musculature of woodpeckers, and the way they use their bills without any head rotation, protects them from rapid skull deceleration and impact-induced bone vibration injury (May et al. 1976, 1979; Kohllöffel 1984). Between the brain and skull woodpeckers have a small subarachnoid space that holds cerebrospinal fluid. The brain of a woodpecker is close to the skull due to low amounts of cerebrospinal fluid in the skull cavity, which is thought to protect the brain by restricting its movement. This small subarachnoid space, in combination with a bill that is held in place by strong muscles and a tongue muscle that extends around the back of the skull over the top of the head inserting at the base of the bill, appears to dampen the vibration and impact woodpeckers receive (May et al. 1976, 1979). Gibson (2006) suggested that the orientation of the brain within the skull, small size of the woodpecker, and short duration of bill-to-tree impacts explain how the adaptive morphology of woodpeckers protects against injury. Specialized morphological adaptations in ear anatomy and musculature, such as a narrowed round window and a specialized dual columellar footplate coupled with the round-window membrane, may act to reduce transient force on the cochlear fluids (Kohllöffel 1984).

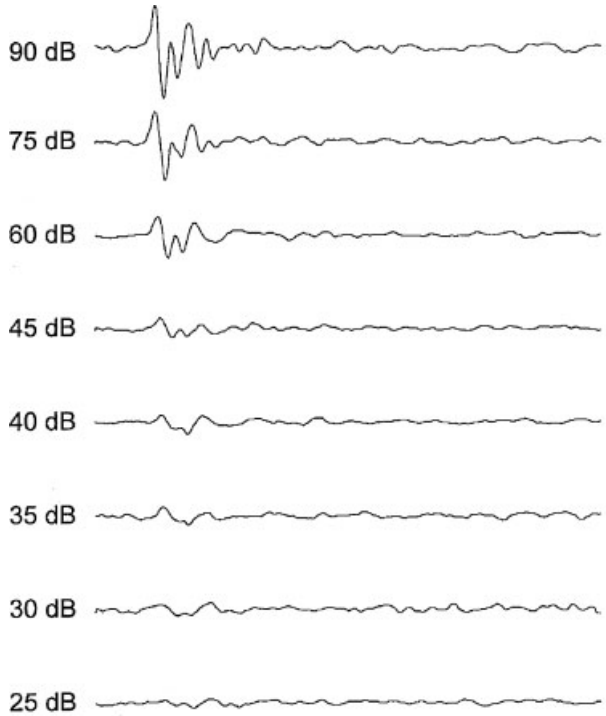

Figure 1. Example of a downy woodpecker's auditory brainstem response, collected as a surrogate for red-cockaded woodpecker hearing sensitivity during 1998 through 2000 at the University of Maryland, College Park, Maryland. dB = decibels.

Effects of Human Disturbance on Animal Populations

Potential impacts of human disturbances on animal populations have been studied for years, but seem to be gaining momentum based on the number and diversity of studies being published in recent years and their emphasis within management and research organizations (e.g., Thiessen 1957; Craig and Craig 1984; Grubb and Bowerman 1997; Kruger et al. 2007; W. Block, U.S. Forest

Service, personal communication). Human disturbance of avian species has received the most attention (e.g., Carrier and Melquist 1976, Grubb and King 1991), though the scope of anthropogenic studies, diversity of disturbance types and species, and behavioral and physiological response parameters has expanded recently (Frid and Dill 2002, Kerr et al. 2004, Mazerolle et al. 2005, Müller et al. 2006, Tarlow and Blumstein 2007). Human presence is probably the most tested disturbance variable (e.g., Blumstein et al. 2003, Holmes et al. 2005). Other sources of potential human-related impacts have been studied, such as roads and vehicles (Prose and Wilshire 1986, Grubb et al. 1998, Forman et al. 2002, Dale et al. 2005), road construction and urbanization (Forman and Alexander 1998, Develey and Stouffer 2001), aircraft overflights (Anderson et al. 1989, Grubb and Bowerman 1997), recreational activities (Grubb and King 1991, Morse et al. 2006, Smith-Castro and Rodewald 2010), habitat loss and fragmentation (Fernández-Juricic et al. 2003), habitat management practices (Ikuta and Blumstein 2003, Yager et al. 2007), natural resource extraction (Kuck et al. 1985, Holthuijzen et al. 1990), military training (Guyer et al. 1995, Delaney et al. 1999, Krausman et al. 2004, Telesco and Van Manen 2006), and sonic booms (Ellis et al. 1991).

Several dependent (e.g., flight initiation, alert and landing distance, temporal displacement or return time, avoidance, physiological response, vigilance) and independent (e.g., body size, type of disturbance, daily and seasonal timing of activity, frequency of occurrence, location of the animal in relation to the stimulus event, conspecific presence, activity at time of disturbance, group size, prior experience) variables have been used to assess effects of human activities on wildlife (Frid and Dill 2002, Nephew et al. 2003, Gill 2007, Tarlow and Blumstein 2007). Most human-animal disturbance studies concentrate on short-term behavioral responses from which it can be difficult to infer significant longer term changes in biologically important factors, such as reproductive success and productivity, population size, or survival (Gill et al. 2001, Beale and Monaghan 2004, but see Bejder et al. 2006). Some researchers have questioned the strength of the relationship between transitory responses and biologically meaningful effects (Hill et al. 1997, Nisbet 2000, Gill et al. 2001). Others suggest that animals showing the strongest responses are not necessarily those most vulnerable to disturbance (e.g., Creel et al. 2002, Stillman and Goss-Custard 2002, Beale and Monaghan 2004). Behavioral indicators generally used to assess tolerance to disturbance (e.g., flight initiation distance) may not necessarily reflect population-level responses (Gill et al. 2001), although others believe that some types of transitory responses (i.e., flush response from active nests) could possibly impact population-level effects if disturbance events are frequent, have a long duration, are loud or have a strong visual component, and impact a large proportion of the population (Delaney et al. 1999).

Two variables that are closely associated with most disturbance studies, but have not been incorporated as readily, are effects of noise on animal populations (Bowles 1995, Delaney et al. 1999, Pater et al. 2009) and mechanisms of animal sound perception (Fay 1988, Fay and Popper 1994, Delaney et al. 1999, Dooling et al. 2000). Researchers had not considered possible effects of military training operations and associated noise levels on red-cockaded woodpeckers until fairly recently, although a large proportion of this species resides on military installations where loud human-based activities frequently occur (Costa 1992). Potential impacts of noise on red-cockaded woodpeckers were first mentioned in the literature by Jackson (1983). Subsequent investigations have compared red-cockaded woodpecker population parameters among different land management practices, training restriction regimes, or nonexperimental military training intensities on various military installations (J. Mobley, unpublished report; J. R. Walters, Virginia Polytechnic Institute and State University, unpublished data; Jackson and Parris 1995; Doresky et al. 2001; Hayden et al. 2002; Perkins 2006). At present, no controlled experimental research has been published on effects of military training and noise on reproductive success, productivity, or nesting behavior of red-cockaded woodpeckers.

We had several primary objectives. First, we sought to determine if implementing the 1996 Army guidelines (reducing the buffer-zone radius around individual trees within each cluster) would reduce red-cockaded woodpecker reproductive success and productivity at individual and population levels. Because red-cockaded woodpeckers are endangered, it was decided by project stakeholders that testing would be initiated on an individual level. To understand potential effects of military training operations on red-cockaded woodpecker populations, we needed to document and understand individual-level effects, if present. Individual-level effects potentially could be linked to population-level effects. Some past studies assumed that population-level effects from human disturbance are present, without these studies effectively showing individual-level effects through detailed monitoring and testing or how individual effects may ultimately be connected to population-level parameters. Our premise was that short-term proximate effects, like flush response and nesting behaviors, can be linked to reproductive success and productivity, which in turn can be linked to potential population-level effects like population sustainability. Additionally, we sought to 2) develop a frequency-weighting function to estimate woodpecker hearing sensitivity; 3) identify factors that affect woodpecker responses to military training operations; 4) develop distance and dose-response thresholds for quantifying woodpecker responses to noise levels and stimulus distances; 5) characterize military training operations through quantification of sound levels, source identification, distance from active woodpecker nests, frequency spectra, duration, and frequency of occurrence; and 6) document baseline woodpecker nesting behavior. We also tested how different frequency-weighting functions (A-weighting vs. woodpecker-weighting) predicted animal response using empirical data from our study, which to our knowledge has not been attempted previously.

STUDY AREA

We conducted our study on Fort Stewart Military Installation (31.88°N, 81.57°W), located in southeastern Georgia 30 km west of Savannah, within Liberty, Long, Bryan, Tattnall, and Evans counties (Fig. 2). The installation had the largest land area (113,064 ha) of any Army installation east of the Mississippi River. It was situated in the Atlantic coastal flatwoods province within a humid, semitropical latitude that averaged 127 cm of rain/year. The average high temperature in January was 16.9°C with a relative humidity of 70%, whereas the July high temperature averaged 34.1°C with a relative humidity of 76% (Delaney

Figure 2. Location of Fort Stewart Army installation, in southeastern Georgia, where we studied red-cockaded woodpecker response to military training operations during 1998 through 2000.

et al. 2002). Approximately 82.6% of Fort Stewart was forested, with 4 main forest types: 1) upland pine stands composed primarily of longleaf (*Pinus palustris*), loblolly (*P. taeda*), and slash pine (*P. elliottii*), 2) mixed pine-hardwood sites, 3) upland hardwood management areas, and 4) forested wetlands. Only 49.1% of Fort Stewart was suitable or potentially suitable red-cockaded woodpecker habitat (Delaney et al. 2002).

The primary mission of Fort Stewart was training and operational readiness of the Third Infantry Division and other nondivision units. The Third Infantry Division was activated in 1975 and redesignated as a mechanized division in 1979 (Hayden 1997*a*,*b*). Training was conducted year-round at Fort Stewart to maintain a combat-ready fighting force. The installation also supported training of regional National Guard and Reserve units, as well as joint training exercises with troops from other installations and DoD Branches (ESMPT 2001). Fort Stewart contained a variety of impact and firing areas (Fig. 3). The central feature of the installation was the artillery impact area (AIA; about 5,200 ha), which was surrounded by artillery firing points varying in distance from a few hundred meters to thousands of meters from the impact area. On the western border of the AIA was the Red Cloud complex, which contained 8 separate ranges. Just south of the AIA were the explosive ordnance disposal area, demolition area, and small-arms impact area (13 live fire ranges, about 2,300 ha). To the east and northeast of the AIA were the combined-arms live fire exercise and Luzon ranges, and 3 smaller aerial gunnery ranges. There were also 7 drop zones located throughout the installation (Hayden 1997*a*,*b*) that were used for parachute training and mock supply drop exercises.

METHODS

Sample Group Selection and Testing

We surveyed and monitored red-cockaded woodpecker groups during April through July of 1998 through 2000. We initially visited clusters to determine occupancy by red-cockaded woodpeckers. We banded adult woodpeckers to determine group size and affiliation using methods similar to those of Walters et al. (1988), although most adults included in our study had been banded before initiation of fieldwork. We monitored woodpecker groups about every 7 to 9 days to record clutch and brood sizes (ESMPT 2001) and to document other reproductive measures (see Woodpecker Response Measures section below). We uniquely color-banded nestlings about 5 to 10 days after hatching. We visited clusters 20 to 25 days after we banded nestlings to determine the number and sex of fledglings (Walters et al. 1988).

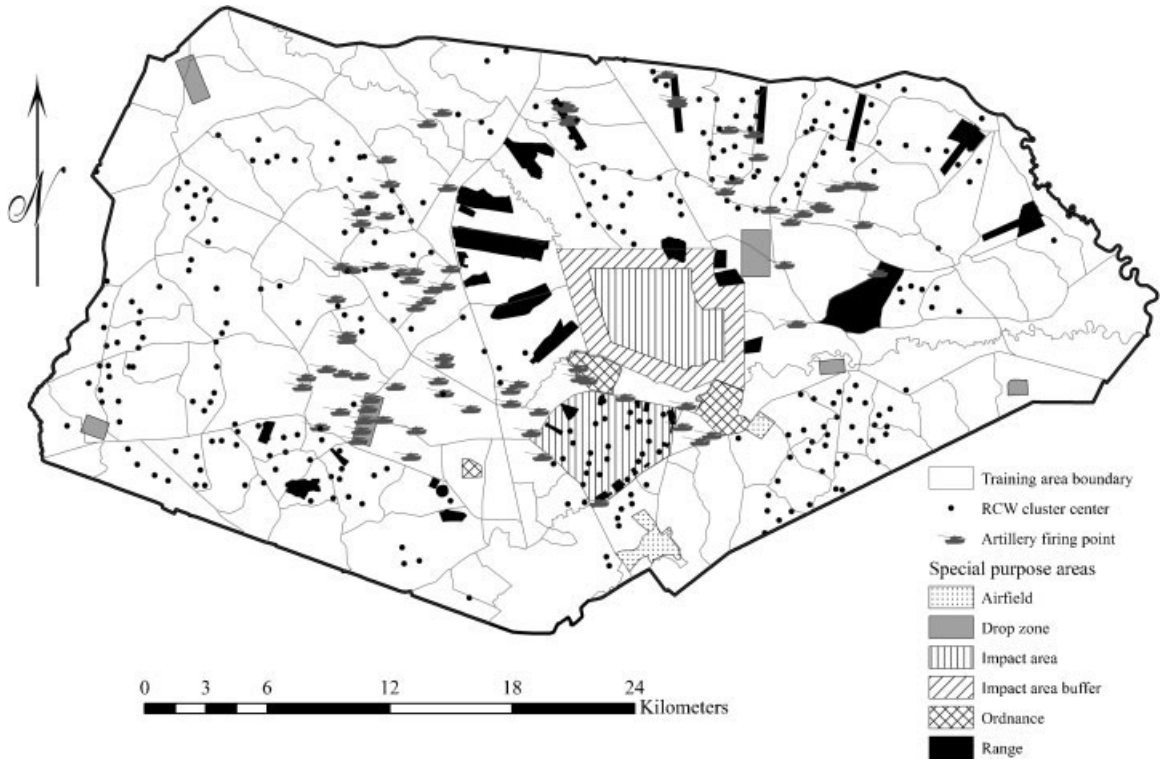

Figure 3. Locations of special-purpose training areas and red-cockaded woodpecker (RCW) clusters subsampled on Fort Stewart, Georgia during 1998–2000.

We selected woodpecker groups from the overall population based on presence of mated pairs, proximity to military training operations, frequency of military training events, relative noise levels received, and habitat suitability. We assigned woodpecker groups to experimental, nonexperimental, or control groups based on information from range control personnel on the type and level of military training operations conducted across the installation and from direct on-site observations and baseline sound profiles. We did not test for differences in habitat parameters among our sample cluster sites. However, based on habitat analysis of suitable woodpecker habitat by Spadgenske (2002) on Fort Stewart at many of the same sites and concomitant with our work, we believe that test sites were comparable in habitat structure and quality across test groups. We monitored 25 nonexperimental groups and 16 control groups of 141 groups that nested in 1998. Group samples numbered 48 experimental, 25 control, and 14 nonexperimental of 165 nesting groups in 1999, and 50 experimental, 27 control, and 31 nonexperimental of 170 nesting groups in 2000. Sample sizes were based on the number of groups that fit protocol criteria.

Woodpeckers within nonexperimental groups were exposed to moderate to high levels of military activity as part of normal training operations (primarily from areas near firing points inward towards the AIA; Fig. 3), although there was no direct control over time of occurrence, number or type of events, or noise level. Nonexperimental groups also received fewer periodic visits by researchers to conduct nest checks, band nestlings, and change videotapes or batteries at video sites. We did not include nonexperimental sites in our overall analysis comparing reproductive success and productivity with experimental and control sites due to our inability to gain consistent access to these locations. Data from these sites provided us important information on the range of military-based sound levels that woodpeckers experienced and on possible responses to those activities.

We selected control sites from the red-cockaded woodpecker population at Fort Stewart (primarily from southeastern and southwestern portions of the installation away from ranges; Fig. 3) due to low numbers of active woodpecker groups on private and state lands in the coastal plain and piedmont province in Georgia (Baker 1995, ESMPT 2001). Woodpeckers within control groups experienced little, if any, military activity and had noise levels near ambient background sound levels. Control groups received levels of researcher presence similar to those of nonexperimental nests, but differed in the amount of military activities and associated noise levels.

We chose experimental groups from areas with low to moderately low disturbance levels to lessen the impact of nonexperimental military activities on experimental testing (primarily from the western portion of the installation, west of firing points; Fig. 3). We monitored nonexperimental noise events during all nesting phases, whereas we conducted experimental tests only during incubation and early portions of the nestling phase when adults were present at the nest for extended periods.

Army personnel presented either artillery simulator blasts or 0.50-caliber blank fire to red-cockaded woodpecker experimental groups under controlled field conditions at distances (m) of 15.2, 30.5, 45.7, 61.0, 76.2, 91.5, 121.9, 152.4, and 243.9 from trees with active nests. Military units approached and departed on a direct path from each test location. Only one simulator was detonated by a soldier during artillery blast events (one exception occurred when a simulator did not fire correctly and a second simulator was used to detonate the first dud simulator), which lasted 10 to 15 seconds. Fifty-caliber machine gun trials required 2 personnel (one to fire the machine gun and one to feed ammunition) and lasted 1 to 5 minutes. Types of sound sources that we tested, number of rounds, duration of experimental tests, and distances were agreed on by installation, USFWS personnel, and researchers before testing. We used artillery simulators and 0.50-caliber blank fire for experimental testing because these sources represented important military training munitions pervasive across the installation.

We randomly presented initial experimental tests at woodpecker groups at 1 of 4 distances (15.2, 30.5, 61.0, or 121.9 m). Due to the short incubation and brooding periods, when adults attended nests for extended periods, we were limited in the number of tests that we could present at each nest. To develop distance and dose-response thresholds, we concentrated testing at these close initial distances in attempts to elicit responses from woodpeckers while not causing nest failure. Due to the short testing period for each nest and the nature of our testing regime over multiple distances using 2 stimulus sources, we could not test for habituation or sensitization of woodpeckers to military training. In addition, we were not permitted to either repeatedly fire noise stimuli at active woodpecker nests or test woodpecker responses across multiple successive days because we did not know how woodpeckers would respond to our initial test plan of single stimulus events with a 4- to 5-day separation. Information on how long to separate tests to reduce or eliminate autocorrelation associated with human disturbance events is not known for this species, or many other wildlife species, so our period of separation was an estimation based on our previous experience and logistical constraints. Logistically, we were not able to return to sites sooner than 4 to 5 days after a test due to our testing schedule at other locations (e.g., Delaney et al. 1999).

We did not test all distances for each noise source or group because woodpecker response dictated which subsequent distances we would test in developing response thresholds. If woodpeckers flushed during initial experimentation, we ended the test for that day and scheduled the next test 4 to 5 days later 15 m to 30 m farther away than the initial test to establish a distance-response threshold. If the initial test did not cause a flush, we presented the next test (4 to 5 days later) 15 m to 30 m closer.

Sound Measurements

Instrumentation and recording.—We used TCD-D8 digital audio tape recorders (Sony Corp. of America, New York, NY) to record sound stimulus events and the exact time and date at which they occurred. We attached Bruel & Kjaer (B&K) Type 4149 condenser microphones measuring 1.3 cm with 7.5-cm windscreens to B&K Model 2639 preamplifiers (B&K, Naerum, Denmark). We mounted each microphone 1 m above the ground and 1 m from the trunk of the nest tree to avoid deleterious effects of sound reflection on the measurement and to avoid disturbing nesting red-cockaded woodpeckers during testing.

We placed the B&K Model 2804 power supply and tape recorders at the base of the nest tree. We recorded a 1.0-kHz,

94-decibel (dB) calibration signal (20-μPa [0.0002 dynes of pressure/cm^2] reference pressure for the dB scale used to measure sound pressure level [SPL] in air; ANSI 2001*b*) from a B&K Type 4250 sound-level calibrating system before and after each recording. Sound pressure level is a metric that is defined as $SPL(dB) = 10\log_{10} (P^2_{rms}/P^2_{ref})$ (ANSI 2004). Here P_{rms} is root-mean-square sound pressure expressed in units such as Pa, and P_{ref} is the reference pressure expressed in the same units. The reference value of 20 μPa is used worldwide for sound measurements in air so that the same sound expressed in dB will be the same anywhere in the world. This calibration signal provided a reference for sound levels and spectra when we later analyzed data. We analyzed all noise data via a B&K Type 2144 frequency analyzer at the United States Army Construction Engineering Research Laboratory.

Acoustical metrics.—Noise, defined as sound (measured in dB) that is undesirable or constitutes an unwarranted disturbance, can alter animal behavior or normal functioning (Crocker 1998). We measured each stimulus sound event by means of ≥1 acoustical metrics to quantify and characterize the sound event in a way that meaningfully correlated with subject response. Animal responses to noise may depend on several acoustic parameters, such as SPL, duration, number of events, frequency distribution of noise energy, wave form (i.e., variation of sound pressure with time), rate of onset, presence of pure tones, and ambient sound (Awbrey and Bowles 1990, Bowles 1995, Delaney et al. 1999). Several of these characteristics varied widely for the types of military noise stimuli woodpeckers encountered during our research.

Measuring SPL or average noise level (LEQ) is problematic for transient noise events of a few to several seconds duration, such as a passage of a vehicle or aircraft, because the choice of measurement period duration affects the metric value reading. We used 2 metrics, sound-exposure level (SEL) and maximum 1-second-equivalent average (LEQ) level, for helicopter, airplane, and vehicle noise events (Environmental Protection Agency 1974, Schultz 1978, Environmental Protection Agency 1982). We noted total duration of the event as the period that we measured 1-second LEQ values within 10 dB of the maximum value. We used SEL to characterize brief transient events such as gunshots. Sound-exposure level is defined as SEL = 10 × LOG10 (E/E0), where E is sound exposure (Harris 1991), defined as the time integral of the square of the sound pressure integrated over the entire event duration, and E0 is the zero reference quantity. Sound-exposure level is generally accepted as an appropriate metric for extremely brief noise events such as blast noise from guns and explosions and mechanical impact noise; the instantaneous peak is also often of interest (Luz 1982). Sound-exposure level and LEQ have been used in previous studies of response to small-arms noise (Sorenson and Magnusson 1979, Hede and Bullen 1982, Buchta 1990).

Ambient sound level.—Ambient sound level is an aspect of the noise environment that is a broadband composite of background sounds, such as wind or sound produced by insects or road traffic (Harris 1991). When obtaining a meaningful measurement of stimulus level, ambient sound is all sound other than the stimulus of interest. Ambient sound has the potential to reduce the effect of noise disturbances by masking the noise stimulus of interest. Furthermore, animals can perceive and respond to noise levels below ambient using cues such as tone (i.e., an auditory sensation having pitch that results from a sound oscillation), spectral characteristics (i.e., representation of amplitude and phase of the components of a complex sound as a function of frequency), and temporal characteristics (e.g., duration, periodicity). In these situations, measurement of the stimulus level is difficult or impossible. Noise-event measurements should include measurements of ambient sound level before and after the noise event, measured as LEQ over a duration of at least several seconds, and a qualitative description of the ambient noise. Measurement and reporting of ambient noise levels are essential for accurate correlation of response with stimulus (Grubb et al. 1998, Delaney et al. 1999). Noise-event level measurements will not accurately measure the stimulus unless stimulus levels are well above the ambient level. For unambiguous measurement, the stimulus should be ≥10 dB above the ambient level to avoid ambient noise contribution to the event-level measurement. Event-level measurements can, and should, be corrected (using logarithmic arithmetic) when the event level is above ambient but <10 dB higher.

Woodpecker Response Measures

The challenge in wildlife disturbance research, especially with threatened and endangered species, is to develop a short-term procedure for inferring impact on long-term survival. We suggest that proximate effects can be linked to individual reproductive measures, which in turn can be linked to population effects (see Delaney et al. 1999). As a specific example, a bird might flush from a nest (a proximate response) in response to a noise event. Flushing could lead to nest failure, especially if the noise and flush response occurred repeatedly. If enough individuals within an area are impacted to cause nest failures, a decline in the population could result. Monitoring is required to determine nesting success within control, experimental, and nonexperimental woodpecker groups.

We recorded a number of reproductive measures for red-cockaded woodpecker groups during each nesting season: 1) reproductive activity; 2) nesting success; 3) fledging success; 4) dates of nest initiation or failure; 5) cause of nest failure, if known; 6) dates for re-nesting attempts; 5) dates for multiple clutch attempts; 7) number of eggs, nestlings, and fledglings produced per occupied/successful nest; 8) percentage of active clusters with nests; 9) percentage change in active clusters and potential breeding groups between years; 10) percentage of woodpeckers changing nests per year; 11) fledgling sex; and 12) number of helpers. Reproductive measures were documented by means of periodic nest checks by installation staff or project personnel, through direct behavioral observation of woodpecker groups at their nest trees, and examination of failed nests.

We documented red-cockaded woodpecker behavior at nest sites by direct observation from camouflaged blinds approximately 35 to 40 m from nests during experimental tests and indirectly through video surveillance at control and nonexperimental nests. We divided the nesting cycle into incubation (eggs present from nest day 0 to 11) and nestling phases (from hatching, nest day 12, to fledging, around nest day 37 to 40). All experimental tests occurred during incubation and the early brooding period of the nestling phase when adults were consistently attending nests. A data session consisted of behavioral observations of ≥1 adult red-cockaded woodpeckers

attending an active nest for ≥1 hours. We could not control for time of day when conducting experimental tests due to logistical constraints associated with soldier availability for testing purposes. Experimental testing occurred during approximately 0730 to 1300 hours 1 to 5 times/week from mid-April to mid-June in 1999 and 2000, whereas we monitored nonexperimental and control nests from mid-April to late June during 1998 through 2000.

We observed woodpecker behavior for ≥30 minutes before and after each experimental noise event. To evaluate woodpecker response to 0.50-caliber blank fire and artillery simulators and link it to pre- and postexperimental behavior, we measured 1) flush frequency (proportion of experimental tests that elicited a flush response from the nest), 2) return time (length of time an adult was away from the nest cavity after flushing), 3) nest attentiveness (proportion of time adult woodpeckers attended the nest cavity through the nesting season), 4) arrivals-prey deliveries (number and rate of prey deliveries to each nest cavity calculated per hour for diurnal and 24-hr periods), and 5) trips (number and duration of trips by attending adult from the nest for diurnal and 24-hr periods).

We primarily used video cameras at control and nonexperimental nest sites to record red-cockaded woodpecker behavior over prolonged periods to reduce data acquisition costs, to avoid potentially disruptive effects of extended human presence (i.e., experimental testing), and to compare baseline nesting behavior and potential response to natural and human-based activities (data not presented). The camera systems also documented woodpecker behavior in areas that could not be safely monitored, such as downrange from firing positions. We primarily monitored nesting behavior and woodpecker responses at experimental nests through direct observation, although we also videotaped a few experimental nests when extra equipment was available.

We attached cameras to tree trunks with adjustable jointed angle-brackets and screws. We mounted cameras at the same level as or slightly above the nest in the nearest practicable tree ≥5 m from the nest tree so as not to disturb incubating woodpeckers. The solid-state 12-volt flexible–circuit board black-and-white cameras (Marshall Electronics, Culver City, CA) were equipped with 12.0-mm lenses. Color cameras (Provideo Corp., Amityville, NY) had 75-mm lenses (use of trade names does not imply endorsement by the U.S. Army to the exclusion of other potentially suitable products). Cameras provided ≥380 lines of resolution and had a minimum sensitivity of 0.45 lx. We mounted black-and-white cameras in waterproof heavy-gauge plastic switch boxes with transparent covers measuring 12.9 cm × 6.7 cm × 4.1 cm. We painted boxes black except for the lens and light-emitting diode area. Color cameras were housed in metal weatherproof containers that measured 30.0 × 9.7 × 9.0 cm. Two ports were threaded into the protective housing, one for the power supply and the second for the video signal (Delaney et al. 1998). We attached power and coaxial cables to a direct current (DC) monitor and battery so we could direct camera placement from the base of the camera tree.

Camera placement required ≥2 people: a climber to position the camera and a person on the ground to check the video signal and placement. We attached a trunk line at the base of the tree and covered it with a camouflaged 1.2-cm diameter hose for protection against rodents. We placed the power and recording station approximately 40 m from the tree to minimize potential disturbance to woodpeckers during tape and battery changes every 2 to 3 days. AG-1070DCP Industrial time-lapse video recorders (Panasonic Corp. of America, Secaucus, NJ) provided approximately 24 to 32 hours of coverage per tape. These 12-volt DC-powered recorders were designed for surveillance applications. We recorded data at a frame rate of 5 frames/second, which allowed time compression during viewing by a factor of about 6. Cameras and video recorders were powered by 2 12-volt 33.0-amp/hour PS-12330 sealed rechargeable batteries (Power-Sonic Corp., San Diego, CA) connected in parallel. Researchers put the recorder, twin batteries, and all connectors inside a weatherproof bin concealed under a camouflaged tarpaulin. We used fully recharged batteries and tapes for each set of recordings. We did not observe any nest abandonment due to camera placement.

Woodpecker Audiogram

An audiogram describes hearing range and sensitivity in terms of threshold sound level as a function of frequency for an animal. Comparing the spectrum of a sound with the audiogram of an animal can aid in noise response data interpretation—e.g., an animal is unlikely to respond to a sound that occurs at frequencies outside of its hearing range. Differences in audiograms among animals can be substantial (Fig. 4). Several studies investigated avian hearing (Saunders et al. 1973, Dooling et al. 2000, Brittan-Powell et al. 2005), including a limited number of studies that were done of other woodpecker species (Winkler and Short 1978, Mahan 1996, Lucas et al. 2002). We found no published literature on hearing sensitivity of red-cockaded woodpeckers.

We collaborated with Dr. R. Dooling and his laboratory at the University of Maryland to measure hearing of a surrogate species, the downy woodpecker (*Picoides pubescens*), a close relative of the red-cockaded woodpecker, to estimate the hearing ability of our target species (Short 1971, Jackson 1994). We measured woodpecker hearing sensitivity by means of ABR techniques that have been used for many years and are proven methods for studying

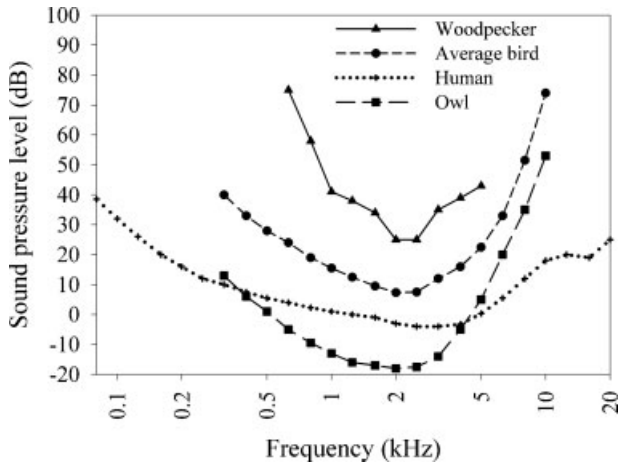

Figure 4. Audiograms showing differences in hearing sensitivity between humans and various bird species. Average bird audiograms are from Dooling et al. (2000); the owl audiogram was developed by Delaney et al. (1999) based on data from Trainer (1946) and Konishi (1973); we developed the woodpecker audiogram in cooperation with the University of Maryland, College Park, Maryland; and human audiograms are based on the International Organization for Standardization 226 (2003). dB = decibels.

sensitivity and functionality of animal auditory systems (Jewett 1970, Dooling et al. 2000, Brittan-Powell et al. 2002, Krausman et al. 2004; Brittan-Powell et al. 2005). We also used hearing data from budgerigars (*Melopsittacus undulates*), for which there are both behavioral and physiological auditory data, to guide interpretation of woodpecker hearing measurement data (Brittan-Powell et al. 2002, Brittan-Powell and Dooling 2004). In addition, we compared the structural vocalizations of downy woodpecker and budgerigars; these spectral characteristics of a species' communication signals are often related to hearing ability. The strongest sensitivity in the audiogram of most animals, particularly passerines and other small birds such as budgerigars, typically coincides with the peak of the average power spectrum of their vocal communication signals (Dooling et al. 2000). Using these data, we inferred an audiogram for small woodpeckers, including red-cockaded woodpeckers.

We used ABR procedures similar to those of Brittan-Powell et al. (2005) to estimate auditory sensitivity of downy woodpeckers. A summary description of the testing facility follows; a detailed description can be found in Brittan-Powell et al. (2005). We controlled sound generation and waveform averaging using TDT hardware modules (a TDT modular rack-mounted system and TDT AP2 Digital Signal Process board) and software (TDT BIOSIG, Gainesville, FL). We generated sound stimuli using TDT SIGGEN software through a DA1 digital-analog converter, PA4 programmable attenuator, and HB6 transducer through JBL professional series speakers (Model 2105H, James B. Lansing Sounds, Northridge, CA).

We anesthetized birds lightly using a mixture of ketamine and diazepam. Once they were sedated, we secured them to a foam pad. We placed standard platinum alloy and subdermal needle electrodes (F-E2, Grass, West Warwick, RI) under the surface of the skin on the scalp. We placed the active electrode at the vertex of the skull and the reference electrode in the skin just dorsal and posterior to the ear that received the auditory stimuli. We placed a ground electrode under the skin on the opposite side of the head from the reference electrode.

To generate woodpecker ABRs we used tones and clicks as stimuli and calibrated them before and after each recording session using a Larson Davis 824 Type 1 sound-level meter (Larson Davis, Provo, UT). We used 5-millisecond alternating-phase-tone bursts with 2-millisecond cosine-ramped rise and fall times delivered at a rate of 20/second. Click stimuli were 0.1-millisecond onset and offset pulses (also alternating in phase) delivered in the same way at a rate of 5/second. We collected responses for 20 milliseconds after each tone burst or click stimulus. We tested birds at the following frequencies (kHz): 0.5, 1.0, 1.5, 2.0, 2.86, 4.0, 5.7, and 8.0. Birds are known to hear at frequencies <0.5 kHz, but are not as sensitive at those frequencies compared with their best hearing range of 1.0 to 5.0 kHz (Dooling et al. 2000, Lucas et al. 2002). We performed hearing-sensitivity testing only down to 0.5 kHz, because the ABR technique is less reliable at lower frequencies.

We estimated threshold response (i.e., the lowest sound intensity at which we observed detectable responses at each test frequency) at each stimulus frequency using peak-to-peak waveform amplitude of the ABR response signal. The hearing threshold at each frequency was taken to be the stimulus level value for which the response signal peak-to-peak amplitude falls to 1 millivolt, which was typically detectable in the presence of ABR noise. The thresholds were, therefore, the intensity values for tones at each frequency of the peak-to-peak amplitude as it fell to a level of +1 millivolt. Such thresholds for tone bursts differed by an absolute value from auditory thresholds determined behaviorally, so we adjusted the threshold sound levels we obtained using auditory-evoked techniques to get an estimate of behavioral thresholds (true thresholds) in woodpeckers. To make this adjustment, we used values from budgerigars, the only species for which both ABR and behavioral data are available.

We obtained archived recordings of vocalizations of downy woodpeckers and red-cockaded woodpeckers from the Cornell University Library of Natural Sounds and the Ohio State University Borror Laboratory of Bioacoustics. These recordings represent several different vocalization types of each species. We used these recordings to investigate the relationship between best hearing sensitivity of woodpeckers and their peak average power spectrum for their vocal communication. This comparison allowed us to examine the suitability of the downy woodpecker as a hearing model for the red-cockaded woodpecker.

Frequency Weighting

A sound metric employed to measure the sounds to which an organism responds should arguably include only acoustical energy that the organism perceives, which we accomplished by means of frequency weighting, an algorithm of frequency-dependent attenuation (a filter) that simulates how hearing sensitivity varies with frequency for the study species (Pater et al. 2009). We can implement weighting by measuring the sound stimulus spectrum in terms of a metric such as 0.33 octave-band SEL (determined by sound-level meters or postprocessing of recordings), applying filter attenuation values to each frequency-band metric level, and then calculating an overall (broadband) weighted metric level by converting each band level to energy units, summing them, and calculating the resultant level.

Weighting filters developed for humans, such as the ubiquitous A and C weightings (Pierce 1989, ANSI 2004), may not be appropriate for animal species whose audiograms differ substantially from those of humans, although A- and C-weighted stimulus levels should be reported as a basis of sound level comparison with other studies where applicable. Few studies have developed frequency-weighting algorithms to represent how animals other than humans perceive sounds and respond to disturbance events (e.g., Delaney et al. 1999, Brittan-Powell et al. 2002, Krausman et al. 2004, Brittan-Powell et al. 2005).

Ideally, a frequency-weighting filter should take into account the overall sound stimulus level, because hearing sensitivity of an organism varies not only with frequency but also with sound level, as is described in detail by equal-loudness curves for humans (Harris 1991, Crocker 1998). We express these curves graphically as sound level measured in dB plotted versus frequency, and we develop the curves by presenting pairs of sounds to a subject, the first of a particular loudness and frequency, and the second of a different frequency. We adjust the level of the second tone until the 2 sounds are subjectively judged by the test subject to be equally loud. The lowest equal-loudness curve is the hearing threshold curve; it passes through 0 dB at about 2,000 Hz, because the zero reference for the atmospheric dB scale is based

on the lowest level sound that can be perceived at the frequency of best sensitivity by a human with good hearing. The sound-level variation in the hearing threshold curve is quite large; at the lower end of the human hearing range, circa 20 Hz, a sound must be about 75 dB louder, and at the upper end, around 20,000 Hz, about 22 dB louder, to sound as loud as the sound level at the frequency of best sensitivity. The curves become flatter at increased loudness; at quite loud levels, variations are less than half as large. The human A-weighting filter mimics a simplified equal-loudness curve at moderate sound levels, whereas the C-weighting filter mimics a high-level equal-loudness curve.

We found no data regarding equal-loudness curves for woodpeckers, or indeed for any animal species other than humans. Consequently, we developed a woodpecker-weighting filter curve based on the only available information, the hearing threshold curve, by simply adopting a filter shape that mimics a smoothed and extrapolated version of the curve. First we slightly smoothed the audiogram shape and then extrapolated to higher and lower frequencies beyond the audiogram data, guided by the shape of a human audiogram. We then changed the sign (i.e., inverted the curve) on the extrapolated audiogram levels at each frequency and added a constant offset value to all of the values sufficient to displace the filter curve to pass through zero at the best hearing frequency (Table 1).

Table 1. Algorithm applied to unweighted sound measurements for the development of the woodpecker-weighting (W-weighting) function applied to data collected on Fort Stewart, Georgia during 1998 through 2000

0.33 octave frequency (Hz)	W-weighting (decibels)
10	−120.7
13	−113.3
16	−105.3
20	−98.3
25	−91.5
32	−84.8
40	−78.0
50	−71.9
63	−65.9
80	−59.9
100	−54.5
125	−49.3
160	−43.8
200	−39.1
250	−34.6
315	−30.2
400	−25.9
500	−22.1
630	−18.4
800	−14.8
1,000	−11.7
1,250	−8.8
1,600	−5.8
2,000	−3.4
2,500	−1.2
3,150	−0.1
4,000	−2.0
5,000	−5.3
6,300	−10.5
8,000	−17.6
10,000	−25.9
12,500	−35.8
16,000	−48.6
20,000	−61.8

Analysis

We used SPSS 8.0 for Windows (SPSS Inc., Chicago, IL) to determine descriptive statistics. We compared analysis of variance (ANOVA) for mean number of eggs, nestlings, and young fledged between the first and second nesting attempts and compared noise levels among stimulus type, year, and distance with 1-way ANOVA. We did not include nonexperimental sites in comparisons of reproductive success and productivity between site variables because we could not adequately monitor these sites due to access issues. We monitored nonexperimental sites when possible to provide a better understanding of the range of potential woodpecker responses to military training and to characterize associated sound levels and frequency spectra of military noise events. Whenever appropriate, we averaged multiple observations at single nests before performing inferential tests so that sample sizes were number of nests examined. We used a 1-tailed Fisher exact test to assess 2×2 contingency tables for variability in nesting success between experimental and control nest sites (Zar 1984).

We generated general linear models and life-table analyses investigating effects of blast impulses on nesting behavior of red-cockaded woodpeckers using SAS/STAT® software (version 9.1.3 of the SAS System for Windows; SAS Institute 2002–2004). We defined statistical significance of effects, where given, as $\alpha = 0.05$. We present means $\pm$ 1 standard error throughout.

Effects of blast stimuli on nest movements.—We analyzed potential effects of military training on nest movements using the SAS GENMOD procedure. The GENMOD procedure fits generalized linear models, as defined by Nelder and Wedderburn (1972). The class of generalized linear models is an extension of traditional linear models that allows the mean of a population to depend on a linear predictor through a nonlinear link function and allows the response probability distribution to be any member of an exponential family of distributions. Classes we used in the ANOVA were treatment (i.e., control, experimental) and year (1998–2001). The model we used for analysis included main effects of treatment and year and the treatment $\times$ year interaction. The dependent variable was change, with 1 indicating that the nest tree within the cluster differed from the previous year and 0 indicating that the nest tree was the same as the previous year. Because dependent variable data were binary (1 = nest change, 0 = no nest change), we used a binomial distribution with a logit-link function. We treated the variable year as a repeated measure on each cluster and performed the analysis using generalized estimating equations (GEEs) with the covariance matrix specified as unstructured.

Some clusters had years with missing data values. We included these clusters in the analysis using the all-available-pairs method, in which we used all nonmissing pairs of data in the moment estimators of the working correlation parameters (Diggle et al. 1994). In addition to this main analysis, we made planned contrasts for control versus experimental estimates for each year separately. For each contrast, we computed the score χ^2 statistic and corresponding *P*-value based on the generalized-score function (Rotnitzky and Jewell 1990, Boos 1992). We used a sample size of 95 clusters in the ANOVA, of which 38 were in the control group and 57 in the experimental group. Of the control group, 23 clusters had no years with missing values, 2

Table 2. Definitions of variables used for information-theoretic modeling analyses of the effects of blast impulse noise on the nesting behavior of red-cockaded woodpeckers on Fort Stewart, Georgia, 1999–2000.

Variable type	Variable name	Type	Levels	Units	Definition
Classes analyzed by:	time frame	Class	30 min 60 min		Interval that a nest was observed before and after a stimulus event
	nestphas	Class	Incubation Nestling		Period before the estimated hatch day, for each subject Period after the estimated hatch day, for each subject
Outcome	p_onnest	Continuous		Dimensionless	Proportion of the interval that an adult was in the nest cavity
	arrivals	Integer		Arrivals at nest	Total no. of times adult arrives at nest within a given time
	flushtime	Continuous		Time (sec)	Time (sec) between stimulus and first emergence of adult from nest
Focal unit	subject	Class	Code no.		Unique no. code identifying the focal unit for each set of measurements, using the cluster identification no., yr, and estimated hatch day
Predictor	treatment	Class	1 2		Nest observation period before stimulus event (preimpulse) Nest observation period after stimulus event (postimpulse)
	stimulus	Class	Artillery Blank		Impulse noise from artillery simulator blast Impulse noise from 0.50-caliber blank fire
	lndistm	Continuous		Dimensionless	Natural log of distance (m) of stimulus impulse noise from nest cavity
	n_helpers	Class	1_helpers 2+_helpers		
	attempt	Integer (1,2)			Denotes whether a nest is a first attempt (1) or a re-nest (2)
Covariates	nestday	Integer		Time (days)	Difference between day of stimulus event and estimated hatchday; Nestday has negative values before estimated hatchday
	blasttime	Continuous		Time (hrs)	Time of day (hrs after midnight) of the stimulus event
	n_young	Integer			Best estimate of no. of eggs (for incubation phase) or nestlings (nestling phase) present in nest at time of stimulus event
	est_hatchday	Integer		Time (days)	Julian day of estimated hatch

had 1 missing value, 9 had 2 missing values, and 4 had 3 missing values. Of the experimental group, 38 clusters had no years with missing values, 3 had 1 missing value, 13 had 2 missing values, and 3 had 3 missing values.

Effects of blast stimuli on nest attendance and arrival rates.—We conducted analyses of effects of blast stimuli at 2 time frames (Table 2). The 60-minute time frame class included only those clusters that we observed for 60 minutes before and after a controlled 0.50-caliber blank fire or artillery simulator event. Data in the 30-minute time frame included those from all clusters we observed 30 minutes before and after stimulus events, with time spans of the time frame = 60 minutes truncated to 30 minutes. Thus, the 60-minute time frame data were a subset of the 30-minute time frame data.

We analyzed outcome variables p_onnest and arrivals at the nest (arrivals; Table 2) using the GENMOD procedure of the SAS/STAT software suite. We modeled the variable p_onnest assuming a binomial distribution with a logit link function, so model results are expressed in terms of log-odds—i.e., as ln[p_onnest/(1 − p_onnest)]. We specified the variable p_onnest in the GENMOD analyses as p_onnest/1, in accordance with the SAS PROC GENMOD events-trials syntax for binomial data. We modeled the dependent variable arrivals assuming a Poisson distribution with a log-link function, so model results are expressed in terms of ln(arrivals). We modeled the class variable treatment as a repeated measure for each nest using the REPEATED statement in GENMOD (SAS Institute 2002–2004), which we used to fit GEE models using repeated measures. We performed analyses separately for incubation and nestling stages. We also performed analyses of data using the 60-minute time frame separately, these being a subset of the nests we used for the 30-minute time frame but at a longer time scale.

We used information-theoretic model selection methods to determine the combination of variable effects on p_onnest and arrivals that were the most parsimoniously supported by the data. This approach provides an alternative to hypothesis testing and multiple *P*-value comparisons as criteria for model selection. We chose a list of candidate models in advance based on theoretical and logical considerations. We then ranked the model outputs using Akaike's Information Criterion (AIC), or other related statistics, based on the model's log-likelihood and the number of parameters estimated, for each candidate model (Burnham and Anderson 2002).

We formulated a set of potential candidate models based on the intrinsic interest of the predictor variables and associated interaction effects (Table 3). We varied effects of treatment, stimulus, distance from the stimulus (lndistm), and their interactions among models. Models 1 to 6 involved no treatment or distance effects (Table 3). Models 7 to 15 involved treatment effects but no distance effects. Models 16 to 24 involved treatment × distance interactions. Models 25 to 33 involved treatment effects and distance effects but no interaction between them. Models 34 to 42 included distance effects but no treatment effects (Table 3). Analyses at the 30-minute time frame additionally included the variables blasttime, nestday, est_hatchday, and n_young as covariates in all models to statistically control for effects of timing of the blast with respect to time of day, day of the nest phase cycle (relative to hatch date), day of the breeding season that hatch occurred, and number of young present in the nest, respectively.

Analyses at the 60-minute time frame, having smaller sample sizes, used only the variable nestday as a covariate to facilitate model convergence and improve statistical power. We chose to use nestday as the covariate because it showed the strongest effect of the 4 covariates we used at the 30-minute time frame (see Results). Additionally, we limited the 60-minute time frame analyses to those models including only 2-variable interactions. We did not include models 15, 21 to 24, 33, and 42 in the 60-minute time frame analyses (Table 3).

Table 3. Effects included in candidate statistical models describing the effects of blast stimuli on red-cockaded woodpeckers nesting behavior on Fort Stewart, Georgia, 1999–2000. We compared models to determine which one most parsimoniously explained variation in the dependant variables nestday and arrivals, using the information-theoretic model selection techniques described in Burnham and Anderson (2002). All models using data with a time frame of 30-min intervals included the variables blasttime, nestday, est_hatchday, and n_young as covariates. All models using data with a time frame of 60-min intervals, except those for p_onnest in the nestling phase that had inadequate sample sizes (see Methods), used the same predictor variables but included only the single variable nestday as a covariate. See Table 2 for definitions of variables.

Model no.	Model (excluding covariates)
1	(intercept only)
2	(intercept and covariates only)
3	stimulus
4	n_helpers
5	stimulus n_helpers
6	stimulusn_helpers
7	treatment
8	treatment stimulus
9	treatment × stimulus
10	treatment n_helpers
11	treatment × n_helpers
12	treatment n_helpers stimulus
13	treatment × n_helpers stimulus
14	treatment × stimulus n_helpers
15	treatment × stimulus × n_helpers
16	treatment treatment × lndistm
17	treatment treatment × lndistm stimulus
18	treatment × stimulus treatment × lndistm × stimulus
19	treatment treatment × lndistm n_helpers
20	treatment treatment × lndistm n_helpers stimulus
21	treatment × n_helpers treatment × lndistm × n_helpers
22	treatment × n_helpers treatment × lndistm × n_helpers stimulus
23	treatment × stimulus treatment × lndistm × stimulus n_helpers
24	treatment × stimulus × n_helpers treatment × lndistm × stimulus × n_helpers
25	treatment lndistm
26	treatment stimulus lndistm
27	treatment × stimulus lndistm
28	treatment n_helpers lndistm
29	treatment × n_helpers lndistm
30	treatment n_helpers stimulus lndistm
31	treatment × n_helpers stimulus lndistm
32	treatment × stimulus n_helpers lndistm
33	treatment × stimulus × n_helpers lndistm
34	lndistm
35	lndistm stimulus
36	stimulus lndistm × stimulus
37	lndistm n_helpers
38	n_helpers lndistm × n_helpers
39	lndistm n_helpers stimulus
40	n_helpers lndistm × n_helpers stimulus
41	stimulus lndistm × stimulus n_helpers
42	stimulus × n_helpers lndistm × stimulus × n_helpers

We regressed the dependent variable (p_onnest or arrivals) on predictor variables using the GENMOD procedure for every model in the appropriate candidate model list for each combination of time frame (30 min or 60 min) and nest phase (incubation or nestling). We calculated the information-theoretic statistic AIC_c for each model using methods described in Burnham and Anderson (2002). We used AIC_c to model goodness-of-fit because total samples were generally small relative to the number of parameters estimated. We then ranked these AIC_c values in order of increasing magnitude and identified the model with the minimum value (implying most support from the data). We then subtracted the minimum AIC_c value from the AIC_c value of each of the models (ΔAIC_c). We considered models with $\Delta AIC_c \leq 2$ to have substantial support from the data. We considered models with higher values of ΔAIC_c to have either equivocal or no support, and we did not consider them further. We also calculated Akaike weights for each model as an indication of relative fit to the data. Our procedures followed guidelines presented in Burnham and Anderson (2002).

We determined a set of models with substantial support from the data for each combination of outcome variables, time frame, and nest phase. Among these, we considered the model with $\Delta AIC_c = 0$ the one with the best fit to the data. Models with similar Akaike weights may be considered nearly equivalent in fit. We then chose a subset of these models for detailed examination, based on which models were of most interest for our study. We considered models with interactions between treatment and any of the other predictor variables of most interest, followed by models with treatment included as a main effect without interactions. We chose models that included many effects over those with fewer but similar effects. We calculated parameter estimates and least-squares means for substantially supported models of greatest interest. For p_onnest during the nestling phase, sample sizes were not adequate to perform analyses for many models due to failure to converge. We analyzed these data by reclassifying nests into classes that were combinations of levels of stimulus and n_helpers, or stimulus_helpers, with 5 levels: artillery_0_helpers, artillery_1_helper, blank_0_helpers, blank_1_helper, and blank_2+_helpers. We then analyzed the data as a factorial ANOVA using the GENMOD procedure, with effects tested being stimulus_helpers, treatment, and stimulus_helpers × treatment. We incorporated no covariates in this analysis.

We analyzed flush times using life-table calculations of the SAS/STAT procedure LIFETEST with the actuarial method option. We treated time from the blast stimulus to the first departure of an adult from the nest using the same calculations as those used for a "time until death" in actuarial analyses. This method has not, to our knowledge, been applied to analysis of flush times but has useful features for that purpose, as it provides a profile of the flush response over time from the blast. Additionally, this method allows use of censored data—i.e., if an adult woodpecker did not depart by the end of the observation period, or if observation was interrupted for other reasons (e.g., end of videotape), then we included the datum in the life-table calculations but handled it as a right-censored observation. We stratified data by combination of stimulus type and distance from the stimulus. We performed analyses separately for incubation and nestling stages. Intervals represent seconds from presentation of the blast stimulus. We performed tests for statistical significance of differences among the strata using the Wilcoxon rank test.

We developed dose-response curves based on red-cockaded woodpecker response to artillery simulator and 0.50-caliber blank-fire events in 1999 and 2000. We performed logistic regression of woodpecker response of unweighted or flat weighted sound levels (dBF; model 2), A-weighted (dBA; model 3), and woodpecker-weighted (dBW; model 4) separately for each stimulus and year because preliminary analyses suggested possible differences between the 2 years. As such, the more conservative assumption would be that years were not homogeneous with

respect to the variables considered. Furthermore, it was not clear a priori whether one dB measure might perform better for artillery and another perform better for blank fire. We also ran a logistic regression with only the intercept included (model 1) in each case for comparison. We compared the 4 models separately for each stimulus type and year using the information-theoretic approach. We present descriptive data on responses to nonexperimental tests. As described earlier, these responses were primarily monitored by video cameras.

Dose-Response Modeling of Flush Response

We can quantitatively express the response of an animal to noise by a dose-response model, an equation or graph describing how probability of a response varies with noise level. Few behavioral response curves have been developed for animals (Bowles et al. 1990, Delaney et al. 1999). It also is important to consider whether an animal is responding to noise or to some other aspect of a potentially disturbing activity. For example, an aircraft presents both auditory and visual stimuli, and some types of noise may be associated with human activity. It may be difficult to separate responses to auditory and visual aspects of the stimulus. In such cases it is important to characterize the stimulus adequately, including the degree to which the noise source was visible to the subject.

Experience with humans has shown that the dose-response relation is different for each type of noise (ANSI 2005). In addition, each animal species may respond differently. Thus, the dose-response model will be specific for each combination of noise type and animal species. For each combination, response variability among individuals requires that we consider statistical significance. We will typically not obtain the entire dose-response curve because extremely high experimental noise levels are not practical for either humans or endangered species. We can obtain the lower portion of the dose-response curve, which will usually provide a delineation of variation of response with noise level over the range of practical interest. In the event that we obtain no proximate responses at tested noise levels, a useful result will be the noise level below which no responses occurred.

We compared woodpecker flush response against 3 weighting functions (i.e., dBF, where no portion of the frequency spectra is filtered; dBA, based on human hearing sensitivity; and dBW, based on woodpecker hearing sensitivity) to determine which frequency-weighting function best predicted animal response. We recorded the blast-stimulus type as artillery or blank fire. We recorded the flush response of the woodpecker from the nest as 1 (flush) or 0 (no flush). We used some clusters during the same year for different distances and stimulus types, and we used some in 1999 and 2000. The unbalanced nature of the data made use of cluster as a subject variable problematic. Therefore, we treated all responses as independent data points in these analyses.

RESULTS

Reproductive Measures

Nesting phases.—Woodpecker first clutches were initiated in 1998 through 2000 during approximately 10 April through 3 June, whereas secondary clutches, groups that re-nested after initial nest failure, were initiated during 2 May through 15 June. Third clutches were initiated during 25 May through 23 June 1999. We observed no third nesting attempts during 1998 or 2000.

Eggs from initial nesting attempts hatched on approximately 21 April through 14 June, whereas eggs from second nesting attempts hatched on 13 May through 26 June. Eggs from third nesting attempts hatched on approximately 5 June through 4 July. We observed young fledging from initial nesting attempts during 20 May through 12 July and during 8 June through 22 July for fledglings from secondary nesting attempts. Successful third nesting attempts fledged during approximately 1 July through 9 July. It is interesting to note that of the 3 third nesting attempts in 1999 (after 2 failed nests at each site), 2 successfully fledged young.

Population dynamics.—Potential breeding groups of woodpeckers increased from 158 in 1997 to 165 in 1998, 174 in 1999, and 181 in 2000, for an overall increase of 14.6% over the 3 years of our project. The number of nesting groups increased from 141 in 1998 to 165 in 1999, and to 170 in 2000, for an overall increase of 20.6%. Potential breeding groups increased steadily on Fort Stewart during this study (Fig. 5). Fledging success rates for individual nests within the overall population remained consistent, averaging 84.4% (range 79.4%–87.7%). During 1998 through 2000, 25.3% (range 20.6%–28.5%) of all initial nesting attempts failed; 62.8% (range 54.3%–70.2%) of woodpeckers re-nested within 2 weeks. Groups that re-nested were as successful and productive as groups that nested only once during each year of our study. We pooled reproductive success and productivity data from initial nesting attempts and re-nesting attempts to determine mean reproductive rates for the overall population each year.

Mean clutch sizes for woodpecker groups for 1998 through 2000 ranged from 2.75 to 3.01 eggs/nest, brood size ranged from 2.01 to 2.22 nestlings/nest, and average number of young fledged ranged from 1.57 to 1.76 young/occupied nest (range 1.83–2.04 young/successful nest). The number and proportion of male and female fledglings varied each year. Numbers of young that fledged each year were 200 in 1998, 290 in 1999, and 279 in 2000. These numbers were comparable to fledge rates in 2001, when 272 young fledged although no experimental noise testing occurred. Woodpeckers fledged a slightly higher proportion of

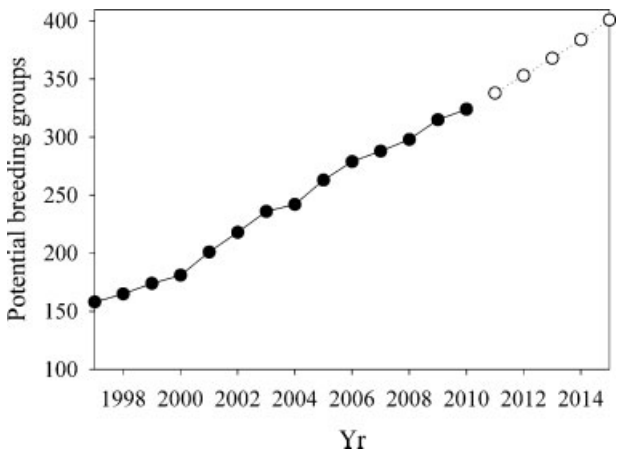

Figure 5. Actual (black circles) and projected (white circles) growth of potential breeding groups of red-cockaded woodpeckers on Fort Stewart, Georgia from 1997 to 2015.

Table 4. Nesting success and reproductive productivity variables for experimental and control red-cockaded woodpecker groups on Fort Stewart, Georgia, 1999–2000.

	Experimental group						Control group					
Response variables	**Single nest**	**SE**	**Re-nest**	**SE**	**Overall**	**SE**	**Single nest**	**SE**	**Re-nest**	**SE**	**Overall**	**SE**
Nesting success (%)	85.0		68.8		82.3		90.9		80.0		88.9	
Eggs/nest	3.06	0.09	2.75	0.19	2.98	0.07	2.93	0.10	2.80	0.36	2.73	0.11
Nestlings/nest	2.16	0.12	1.75	0.19	1.89	0.11	2.18	0.11	1.90	0.38	1.91	0.13
Young/occupied nest	1.81	0.12	1.25	0.23	1.54	0.12	1.82	0.12	1.80	0.39	1.57	0.13

males than females in 1998 (53.5%) and 1999 (53.1%), whereas we observed the reverse in 2000 (46.2%) and 2001 (47.4%).

Of the 58 groups that received experimental testing in 1999 and 2000, 79 of the 96 nesting attempts (82.3%) were successful in fledging young. Of these 96 nesting attempts, 28 initially failed. Of the 28 groups that initially failed during their first nesting attempt, we found 16 re-nesting within 2 weeks, with 68.8% successfully fledging young. Experimental groups that nested only once were successfully in 68 of 80 nesting attempts (85.0%). Experimental groups that re-nested were as successful (Fisher Exact Test, $P = 0.08$; 68.8% for groups that re-nested versus 85.0% for initial nesting attempts) and productive as experimental groups that nested only once (Table 4). We observed no difference in number of eggs ($F_{1,94} = 0.42$, $P = 0.15$), number of nestlings ($F_{1,94} = 2.92$, $P = 0.14$), or number of fledglings ($F_{1,94} = 0.07$, $P = 0.053$) between experimental groups that re-nested and ones that nested only once on a per nest basis. All reproductive measures are shown on a per nest basis. Therefore, we pooled data before determining reproductive rates for overall sample groups. We pooled data because, although some differences neared significance, combining the data enabled larger sample sizes. Pooling resulted in a more conservative test of the hypothesis that disturbance had no effect because any bias introduced by combining would be toward lower success in experimental groups.

Of the 34 control groups monitored in 1999 and 2000, 49 of the 54 nesting attempts (90.9%) were successful in fledging young (Table 4). Of these 54 initial nesting attempts, 14 failed. This failure rate was not different from initial failure rates for experimental groups (Fisher Exact Test, $P = 0.14$). Ten of the 14 RCW groups that initially failed during the first nesting attempt re-nested with 80.0% successfully fledging young. Control groups that re-nested were as successful (Fisher Exact Test, $P = 0.24$; 80.0% for groups that re-nested versus 90.9% for initial nesting attempts) and productive as control groups that nested only once (Table 4). We observed no difference in number of eggs ($F_{1,52} = 4.78$, $P = 0.64$), number of nestlings ($F_{1,52} = 4.79$, $P = 0.33$), or number of fledglings ($F_{1,52} = 6.33$, $P = 0.95$) between control groups that re-nested and groups that nested only once. Therefore, we pooled data before determining reproductive rates for the overall sample group. The proportion of experimental nesting attempts that were successful did not differ from that of successful control nests (Fisher exact test, $P = 0.11$; Table 4). Experimental and control groups did not differ in number of eggs ($F_{1,90} = 4.16$, $P = 0.058$), number of nestlings ($F_{1,90} = 1.06$, $P = 0.88$), or number of fledglings ($F_{1,90} = 1.00$, $P = 0.88$) from 1999 to 2000.

We also compared 1999 and 2000 reproductive data from experimental groups with 2001 reproductive data for these same groups, after experimental testing had finished. We found no differences in the proportion of groups that initially failed in their nesting attempts (Fisher exact test, $P = 0.20$) or the proportion of re-nesting groups that nested successfully (Fisher exact test, $P = 0.25$) between experimental test years (1999 and 2000) and 2001. We found no difference in number of eggs ($F_{1,90} = 5.43$, $P = 0.86$), number of nestlings ($F_{1,90} = 5.69$, $P = 0.41$), or number of fledglings ($F_{1,90} = 2.61$, $P = 0.72$) between experimental test years and postexperiment reproductive data.

Based on a preliminary power analysis done in 1998 before our study, we estimated that a group size of 95 experimental and 95 control red-cockaded woodpecker groups would be necessary to reach an adequate power level of 0.80 (Fig. 6). The power analyses in 1999 and 2000 showed only a 0.33 to 0.41 probability of detecting a 25% decrease in reproductive productivity in control nest sites ($\alpha = 0.05$; 2-tailed test). Power decreased to 0.23 to 0.29 for detecting a 20% decrease in reproductive productivity, to 0.15 to 0.18 for a 15% decrease, and down to 0.09 to 0.11 for detecting a 10% decrease in reproductive productivity between disturbed and control red-cockaded woodpecker groups.

Hearing

Woodpecker audiogram.—The best sensitivity in the audiogram of most animals, particularly passerines and other small birds such as budgerigars, typically coincides well with the peak of the

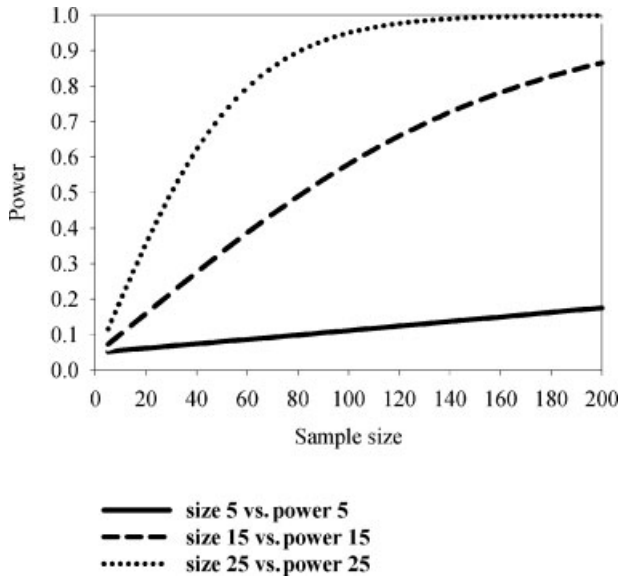

Figure 6. Relationship between sample size and power comparing experimental and control reproductive parameters for red-cockaded woodpeckers on Fort Stewart, Georgia during 1999 through 2000. Lines represent relationships between sample size and power for detecting 5%, 15%, and 25% differences in reproductive characteristics.

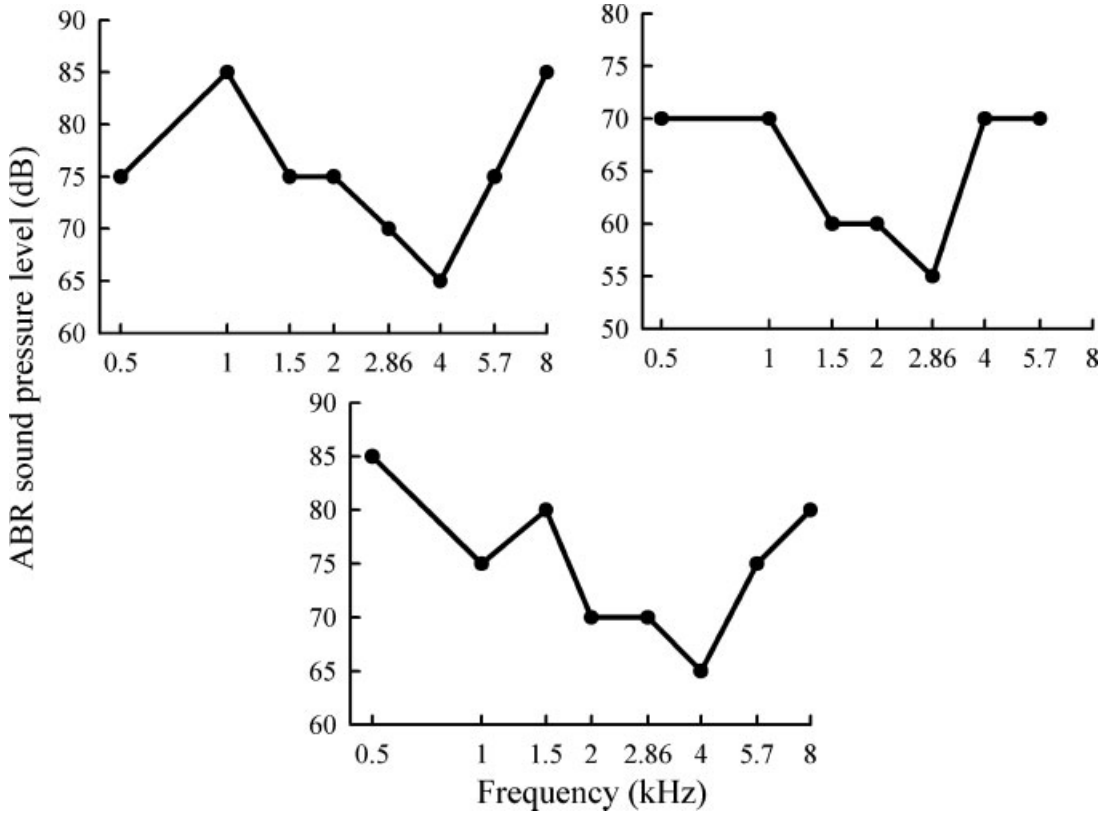

Figure 7. Audiograms for 3 individual downy woodpeckers obtained using auditory brainstem response (ABR) techniques during 1998 through 2000 at the University of Maryland, College Park, Maryland. dB = decibels.

average power spectrum of their vocal communication signals (Dooling et al. 2000). Electrophysiological audiograms from 3 downy woodpeckers (Fig. 7) provided the best estimate of their hearing abilities. We developed an average downy woodpecker audiogram from these 3 individuals (Fig. 8) and compared it to an average behavioral audiogram for 20 species of small passerine birds, and we adjusted the average downy woodpecker audiogram for the absolute difference between physiological and behavioral curves in budgerigars (a 35-dB difference). We observed some variability in data across individuals (Fig. 7), suggesting that further tests with a larger sample are warranted. Woodpeckers are most sensitive in the 1.5- to 4.0-kHz range. Sensitivity appeared to drop off quickly at frequencies of <1.5 kHz and >4.0 kHz (Fig. 9). Downy woodpeckers also appear to be less sensitive in absolute terms than the typical passerine. We did not display data for tones at 300 Hz on these audiograms, as woodpeckers exhibited no sensitivity at this lowest tested frequency (all peak-to-peak waveform amplitudes were <1 millivolts). Woodpeckers also showed little sensitivity to 8,000-Hz tones using the ABR technique. Behavioral thresholds for budgerigars are typically 50 dB to 60 dB higher at this frequency than at their best frequency (approx. 2,860 Hz).

Vocalizations.—We analyzed average power spectra for 3 common vocal signals and the percussive drumming of the downy woodpecker, as well as 2 vocalizations of the red-cockaded woodpecker (Fig. 9). We found much lower frequencies present in the drum. Most energy in the calls of these woodpeckers was spread across a broad range of high frequencies (2.0–6.0 kHz) compared with songs and calls of most passerines (2.0–4.0 kHz).

We superimposed the average spectra for the drum and call note of the downy woodpecker over the average ABR audiogram from the 3 test individuals (Fig. 10). Although the drum has frequencies generally lower than the best sensitivity of the audiogram,

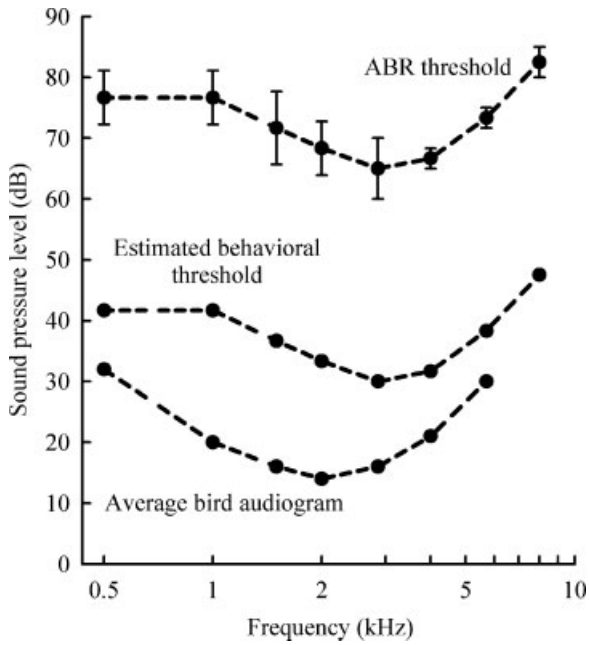

Figure 8. Average auditory brainstem response (ABR) audiogram for 3 downy woodpeckers (top) obtained at the University of Maryland, College Park, Maryland during 1998 through 2000. Audiogram adjusted for absolute difference between electrophysiological and behavioral thresholds (middle) and average passerine audiogram (estimated using behavioral techniques). dB = decibels.

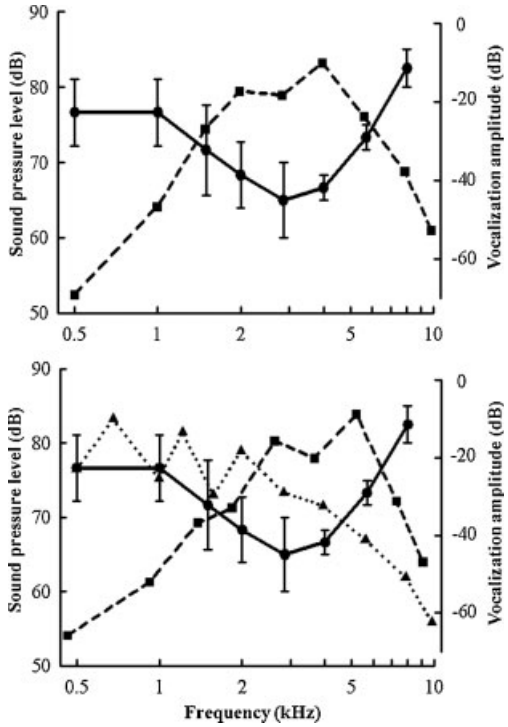

Figure 9. Average audiogram for 3 downy woodpeckers with superimposed average power spectra for the call note of red-cockaded woodpeckers, average audiogram for 3 downy woodpeckers with superimposed average power spectra for the percussive drum, and the call note vocalization of downy woodpeckers collected at the University of Maryland, College Park, Maryland during 1998 through 2000.

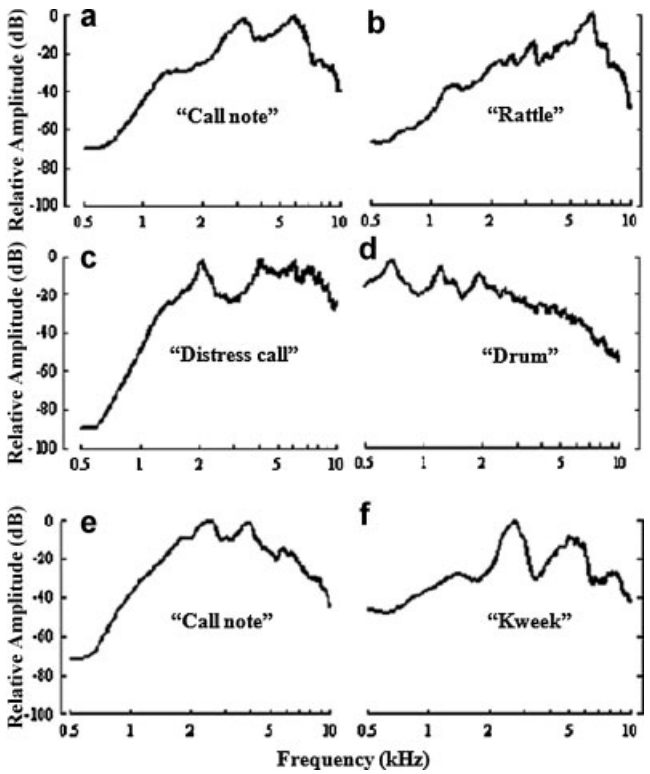

Figure 10. Average power spectra for 3 common downy woodpecker calls (a–c), the drum (d), and two common vocalizations (e, f) of the red-cockaded woodpecker examined at the University of Maryland, College Park, Maryland during 1998 through 2000.

peak frequency of the call note corresponded well to the audiogram best sensitivity. We also superimposed the same average downy woodpecker audiogram with the call note of the red-cockaded woodpecker (Fig. 10). Once again, there was a good correspondence between peak power in the average spectrum of this vocalization and best sensitivity of the audiogram. The resulting audiogram showed woodpecker hearing sensitivity to be poorer at high and low frequencies compared to humans (Fig. 4), but the general shapes of the audiogram curves were similar.

Effects of Blast Stimuli on Woodpecker Nesting Behavior

We conducted 206 experimental tests on 58 woodpecker groups using artillery simulators (Table 5; Delaney et al. 2002) and 0.50-caliber blank fire (Table 6; Delaney et al. 2002) in 1999 and 2000. Artillery simulator and 0.50-caliber blank-fire events generated comparable unweighted noise levels during the 1999 and 2000 field seasons, but when we examined W-weighted levels for these events, we found that 0.50-caliber blank-fire events were louder and less variable than artillery simulators at comparable distances (Tables 5 and 6). In 1999, woodpeckers flushed from their nests 17.1% more often during 0.50-caliber blank-fire tests than during artillery simulator tests at comparable distances (Fisher exact test, $P = 0.03$). In 2000, we observed that 0.50-caliber blank-fire events were 4.2 dB (unweighted) louder on average than artillery simulators at comparable distances during experimental testing (Fisher exact test, $P = 0.03$; Tables 5 and 6). However, higher noise levels during 0.50-caliber blank firing testing did not translate into greater flush response levels for woodpeckers in 2000. In 2000, woodpeckers flushed at similar rates during 0.50-caliber blank-fire tests (53.3% across all tests) compared with artillery simulator tests (51.8% across all tests) over comparable distances (Fisher exact test, $P = 0.15$).

The score statistics from type 3 GEE ANOVAs, which examine the effects of blast stimuli on nest movements, were as follows: treatment, $\chi^2_1 = 3.29$, $P = 0.070$; year, $\chi^2_3 = 1.15$, $P = 0.766$; and treatment × year, $\chi^2_3 = 2.95$, $P = 0.400$. None of these values were statistically significant at the $\alpha = 0.05$ level, although the treatment effect came notably close to significance. Overall, a higher proportion of red-cockaded woodpeckers changed nests between consecutive years in the experimental group than the control group. However, the year after the final year of blast treatments, 2001, was the only year for which the difference was significant ($\alpha = 0.05$; Table 7). A higher proportion of birds changed nests between 2000 and 2001 in the experimental group (0.40) than in the control group (0.19).

Thirty-minute time frame.—Sample sizes for analysis of effects of blast stimuli on nest arrival and nest attendance were higher for the incubation phase than for the nestling phase (Table 8). For arrivals during the incubation phase, strong effects of treatment, stimulus, and n_helpers were apparent (Table 9). The top-ranking model was the simple treatment + n_helpers model (model 10). However, the models of most interest were model 14 (see Table 3 for descriptions of models), with a strong treatment × stimulus interaction, and model 11, with a strong treatment × n_helpers interaction. Model 14 showed that stimulus type had a strong influence on the effect of the treatment: it

Table 5. Number, distance, and noise level of experimental artillery simulator tests conducted at active red-cockaded woodpecker (W) nests during 1999 through 2000 on Fort Stewart, Georgia. A dagger signifies the event where 2 artillery simulators were detonated together to destroy 1 dud.

Distance (m)	Noise events	Data sessions	No. of flushes	Flush frequency (%)	Noise levels (SEL [dB])[a]		Ambient LEQ (dB),[b] W-weighted
					Base unweighted	Base W-weighted	
15.2	6	6	5	83.3	93–107	79–91	27–35
30.5	33	33	20	60.6	89–105	71–91	23–37
45.7	8	8	3	37.5	80–100	70–82	24–31
61.0	29	29	11	37.9	81–104	66–89	23–32
76.2	2	2	1	50.0	74–97	66–75	29–34
91.4	13	13	4	30.8	74–101	64–83	27–30
121.9	16	16	1	6.3	73–99	61–82	30–39
152.4	1	1	0	0.0	74	67	30
243.8	2	1	0	0.0	98†	66	31
Totals	110	109	45				

[a] SEL = sound-exposure level; dB = decibels.
[b] LEQ = average noise level.

Table 6. Number, distance, and noise level of experimental 0.50-caliber blank-fire tests conducted at active red-cockaded woodpecker (W) nests during 1999 through 2000 on Fort Stewart, Georgia.

Stimulus distance (m)	Noise events	Data sessions	No. of flushes	Flush frequency (%)	Noise levels (SEL [dB])[a]		Ambient LEQ (dB),[b] W-weighted
					Base unweighted	Base W-weighted	
15.2	69	5	4	80.0	96–108	85–98	26–28
30.5	328	26	17	65.4	91–106	81–97	30–34
45.7	108	4	2	50.0	88–101	74–90	31–42
61.0	384	30	14	46.7	84–100	69–87	25–39
76.2	51	3	3	100.0	89–93	78–82	27–32
91.4	120	15	8	53.3	80–95	68–82	28–36
121.9	94	12	2	16.7	84–89	65–79	28–35
152.4	24	1	0	0.0	81–87	64–69	32
243.8	21	1	0	0.0	61	42	35
Totals	1199	97	50				

[a] SEL = sound-exposure level; dB = decibels.
[b] LEQ = average noise level.

Table 7. Least-squares means from the general linear models binomial analysis of variance of red-cockaded woodpecker nest tree changes on Fort Stewart, Georgia, 1999–2000. The model used for analysis included the main effects of treatment and year and a treatment × year interaction. The dependent variable was the proportion of woodpeckers-changes-nest trees: A) by treatment (control vs. experimental [exp.]) for each year and B) marginal proportions over all years. *P*-values are for contrasts of control vs. experimental groups. Proportions are back-transformed from the logits used.

Effect	Year	Treatment	χ^2_1 df	*P*-value	Proportion changing-nest tree	95% CI	
						Lower	Upper
A) Treatment	1998	Control	0.65	0.422	0.173	0.074	0.353
		Exp.			0.250	0.145	0.398
	1999	Control	0.07	0.785	0.269	0.139	0.457
		Exp.			0.241	0.139	0.383
	2000	Control	1.58	0.209	0.205	0.097	0.381
		Exp.			0.330	0.217	0.467
	2001	Control	4.41	0.036	0.188	0.087	0.359
		Exp.			0.402	0.275	0.543
B) Overall		Control	3.31	0.069	0.206	0.138	0.296
		Exp.			0.302	0.242	0.370

reduced arrivals at the nest by 41% when the stimulus was blank fire, but only by 23% when the stimulus was artillery fire (Table 10). Model 11 showed that reduction of arrivals by blast stimuli was pronounced (40%) when no helpers were present, but the strength of this effect decreased as number of helpers increased and was negligible (6%) for nests with ≥2 helpers. Among covariates, nestday generally had a strong positive statistical effect on arrivals (Table 11), meaning that arrivals increased as the day of hatch approached. Variables blasttime and est_hatchday had generally weaker negative effects (Table 11). Thus, arrivals tended to decrease as time of day progressed from early morning to early afternoon and tended to be lower for nests that hatched later in the breeding season. The variable n_young had no detectable effect on arrivals.

For arrivals during the nestling phase, only model 7 had substantial support, with a strong treatment main effect. Least-squares means from this model showed an overall reduction in arrivals of 25% due to the blast treatment (Table 10). No

Table 8. Sample sizes for the number and type of observation periods at red-cockaded woodpecker nests used in the study on Fort Stewart, Georgia, 1999–2000. The nests with data at the 60-min time frame are a subset of the nests with data at the 30-min time frame. See Table 2 for definitions of variables.

Time frame	Nest phase	Stimulus	No. of helpers			Grand total
			0	1	2	
30 min	Incubation	Artillery	39	25	7	71
		Blank	17	31	5	53
	Incubation total		56	56	12	124
	Nestling	Artillery	13	8	2	23
		Blank	13	14	3	30
	Nestling total		26	22	5	53
30 min total			82	78	17	177
60 min	Incubation	Artillery	18	14	3	35
		Blank	8	11	4	23
	Incubation total		26	25	7	58
	Nestling	Artillery	4	5	0	9
		Blank	4	3	3	10
	Nestling total		8	8	3	19
60 min total			34	33	10	77

Table 9. Information-theoretic ranking of models with substantial support (difference in the second-order Akaike Information Criterion for the model from the smallest such value in the set of candidate models [ΔAIC_c] < 2) estimating effects of experimental stimulus events on arrivals and nest attendance (p_onnest) rates of red-cockaded woodpeckers at nests on Fort Stewart, Georgia, 1999–2000.

Time frame	Variables	Nest phase	ΔAIC_c	w_AIC_c[a]	Model no.	Deviance	df	Deviance df	K[b]	Model[c]
30 min	arrivals	Incubation	0.000	0.201	10	185.9	240	0.77	8	t, h, b, n, e, y
			0.318	0.172	14	181.9	238	0.76	10	t × s, h, b, n, e, y
			0.567	0.152	12	184.3	239	0.77	9	t, h, s, b, n, e, y
			1.568	0.092	11	183.1	238	0.77	10	t × h, b, n, e, y
		Nestling	0.000	0.356	7	70.2	100	0.70	6	t, b, n, e, y
	p_Onnest	Incubation	0.000	0.629	1	58.3	247	0.24	1	intercept
		Nestling	0.000	0.872	1	30.5	105	0.29	1	intercept
60 min	arrivals	Incubation	0.000	0.350	10	119.0	111	1.07	5	t, h, n
			0.905	0.223	12	117.7	110	1.07	6	t, h, s, n
			0.990	0.214	14	115.5	109	1.06	7	t × s, h, n
		Nestling	0.000	0.179	4	26.4	34	0.78	4	h, n
			0.063	0.174	10	23.8	33	0.72	5	t, h, n
			1.052	0.106	7	30.0	35	0.86	3	t, n
			1.289	0.094	2	32.6	36	0.90	2	n
	p_onnest	Incubation	0.000	0.360	1	13.6	115	0.12	1	intercept
			1.816	0.145	34	13.3	111	0.12	3	d, n
			1.942	0.136	2	13.5	114	0.12	2	n

[a] Corresponding Akaike weight for that model.
[b] No. of estimable parameters in the model.
[c] t = treatment, s = stimulus, h = n_helpers, d = lndistm, b = blasttime, n = nestday, e = est_hatchday, y = n_young. See Table 2 for explanation of variables.

interactions of treatment with other variables were supported by the data. Among covariates, only nestday had consistently strong positive statistical effects on arrivals (Table 11). The value of the nestday parameter was approximately 0.05 to 0.06 among the models. Back-transforming these parameters from the Poisson logarithmic models, this meant that arrivals tended to increase by 5%–6% of its value each day after the hatch date. For p_onnest during the incubation and nestling phases, the only model with substantial support was the intercept-only model, model 1 (Table 9). Intercept-only models imply that, for both incubation and nestling phases, p_onnest was best characterized by one mean value, regardless of predictor variable values. Means and 95% confidence intervals for p_onnest were 0.85 (0.82, 0.87) for the incubation phase and 0.75 (0.70, 0.79) for the nestling phase.

Sixty-minute time frame.—For arrivals during the incubation phase, strong effects of treatment, stimulus, and n_helpers were apparent. The top-ranking model was the simple treatment + n_helpers model (model 10). However, the model of most interest was model 14, which included a treatment × stimulus interaction and a main effect of n_helpers. The treatment × stimulus interaction we saw at the 30-minute time frame was apparent also at the 60-minute time frame. No treatment × n_helpers interaction was supported by the data. The variable nestday was the only covariate used and generally had a positive statistical effect on arrivals (Table 12), weaker but consistent with the result for arrivals at the 30-minute time frame. For arrivals during the nestling phase, the model of most interest was model 10, which included a strong effect of n_helpers, not apparent for nestlings at the 30-minute time frame, and a weaker treatment main effect, with no interactions. Blast treatments reduced arrivals by about 20% and showed a general increase in arrivals with number of helpers (Table 10). The covariate nestday was strongly positive with arrivals increasing with number of days after hatch (Table 12).

For p_onnest during the incubation phase, the model with the most substantial support was the intercept-only model, model 1.

Table 10. Estimated mean values of number of arrivals back-transformed from ln(arrivals) from selected Poisson regression models based on data from red-cockaded woodpecker nests on Fort Stewart, Georgia, 1999–2000. Percentage reduction in no. of arrivals is shown for effects that include the blast impulse treatment. See Table 2 for definitions of variables.

								95% CI		
Time frame	Model no.	Nest phase	Effect	Stimulus	N_helpers	Treatment	Arrivals	Lower	Upper	Percent reduced
30 min	11	Incubation	treatment × n_helpers		0_helpers	1	2.26	1.98	2.58	
						2	1.35	1.06	1.70	40.4
					1_helper	1	2.68	2.40	2.99	
						2	1.94	1.58	2.37	27.7
					2 + _helpers	1	2.93	2.43	3.54	
						2	2.75	2.27	3.34	6.1
	14	Incubation	treatment × stimulus	Artillery		1	2.69	2.44	2.98	
						2	2.09	1.76	2.46	22.6
				Blank		1	2.68	2.35	3.06	
						2	1.57	1.30	1.89	41.4
	7	Nestling	treatment			1	3.48	3.15	3.84	
						2	2.63	2.27	3.04	24.5
60 min	14	Incubation	n_helpers		0_helpers		2.86	2.36	3.47	
					1_helper		3.87	3.28	4.57	
			n_helpers		2 + _helpers		3.74	2.85	4.90	
			treatment × stimulus	Artillery		1	4.08	3.37	4.95	
						2	3.37	2.68	4.24	17.4
				Blank		1	4.13	3.57	4.78	
						2	2.51	2.02	3.12	39.2
	10	Nestling	n_helpers		0_helpers		4.51	3.69	5.51	
					1_helper		6.70	5.64	7.96	
					2 + _helpers		5.83	5.11	6.65	
			treatment			1	6.25	5.51	7.09	
						2	5.03	4.25	5.95	19.5

Model 34, which included distance as a factor, also had support. Examination of the parameters of this model revealed that neither lndistm nor nestday parameters differed from zero at the 0.10 level (Table 12). The means and 95% confidence intervals for p_onnest were 0.88 (0.85, 0.90). For p_onnest during the nestling phase, the GENMOD factorial ANOVA yielded no significant effects of treatment, stimulus_helper, or treatment × stimulus × helper at the 0.05 level, or even the 0.1 level, which may be a function of inadequate sample sizes but is consistent with the lack of any effects of treatment, stimulus, or n_helpers seen for p_onnest in general.

Flush frequency of red-cockaded woodpeckers increased as stimulus distance decreased, regardless of stimulus type or year (Tables 5 and 6). At distances of ≤122 m, 0.50-caliber blank fire elicited (Fisher exact test, $P = 0.057$) a higher proportion of flushes (52.6%) than comparably distant artillery simulators (42.1%). The life-table analysis of flush response showed that the response time for woodpeckers to flush from nest trees due to a stimulus event (flush time) showed significant differences among stimulus type-distance strata during both incubation (Wilcoxon $\chi^2_5 = 13.23$, $P = 0.021$; Fig. 11) and nestling (Wilcoxon $\chi^2_5 = 12.29$, $P = 0.031$; Fig. 12) phases. A large proportion of flush responses occurred within the first 5 seconds after the stimulus event began for both stimulus types (Figs. 11 and 12). Time to flush during both the incubation and the nestling phases was shortest in response to artillery blasts 15 m to 30 m from nests, followed by blank fire at 46 m to 61 m, and then blank fire at 15 m to 30 m (incubation phase only). Thus, the observed flush response was strongest overall for short-range artillery fire and midrange blank fire. The overall strength of the flush response among the treatments at the midpoint of the first 5-second interval appeared to be stronger during the nestling phase (with proportions of birds remaining on the nest ranging from 20% to 70%) than during the incubation phase (with proportions of birds remaining on the nest ranging from 45% to 87%). An exception to this pattern was observed for birds in the nestling phase subjected to artillery fire at >61 m. These birds appeared to exhibit no flush response to the artillery stimulus, with 100% of birds remaining on the nest. Woodpeckers returned to nests within 4.4 minutes on average after being flushed by artillery simulators, returning in ≤16.2 minutes overall (Fig. 13). Return times were slightly higher for 0.50-caliber blank-fire tests, averaging 6.3 minutes and returning in ≤26.8 minutes overall.

Flush Response to Nonexperimental Events

We recorded 2,845 noise events in 156 data sessions at 50 red-cockaded woodpecker groups from 1998 to 2000 (Tables 13–18; see appendix D in Delaney et al. 2002). Small-caliber live fire events were recorded most frequently in 1998 through 2000, followed by large-caliber live fire events, missiles, military helicopters, military/civilian vehicles, and artillery/grenade simulators. Multiple noise events and stimulus types were usually recorded during nonexperimental data sessions. We also monitored 40 control groups for the purpose of obtaining baseline behavioral information against which to judge proximate response at experimental groups.

Small-caliber live fire.—We recorded 1,930 small-arms live fire noise events during 29 data sessions at 14 woodpecker groups during 1998 through 2000 (Table 13). We did not observe any

Table 11. Analyses of generalized estimating equation (GEE) parameter estimates and associated empirical standard error (SE) estimates for models at a 30-min time frame based on data from red-cockaded woodpecker nests on Fort Stewart, Georgia, 1999–2000. We modeled no. of arrivals using Poisson regression and p_onnest using logistic regression. Normal deviate statistic *Z* and associated *P*-values test the difference of the parameter from zero. See Table 2 for definitions of variables.

Dependent variable	Model no.	Nest phase	Parameter	Level 1	Level 2	Estimate	SE	95% CI Lower	95% CI Upper	*Z*	*P*-value
arrivals	14	Incubation	intercept			0.25	0.76	−1.24	1.74	0.33	0.74
			treatment × stimulus	1	Artillery	0.54	0.11	0.33	0.76	4.90	<0.01
			treatment × stimulus	1	Blank	0.54	0.11	0.31	0.76	4.73	<0.01
			treatment × stimulus	2	Artillery	0.29	0.13	0.02	0.55	2.13	0.03
			treatment × stimulus	2	Blank	0.00	0.00	0.00	0.00		
			n_helpers	0_helpers		−0.46	0.10	−0.66	−0.26	−4.58	<0.01
			n_helpers	1_helper		−0.18	0.09	−0.36	−0.01	−2.08	0.04
			n_helpers	2+_helpers		0.00	0.00	0.00	0.00		
			blasttime			−0.05	0.03	−0.09	0.01	−1.79	0.07
			nestday			0.05	0.01	0.02	0.08	3.80	0.01
			est_hatchday			0.01	0.01	0.00	0.02	1.96	0.05
			n_young			−0.01	0.06	−0.12	0.12	−0.05	0.96
arrivals	11	Incubation	intercept			0.70	0.75	−0.77	2.16	0.93	0.35
			treatment × n_helpers	1	0_helpers	−0.20	0.12	−0.43	0.04	−1.63	0.10
			treatment × n_helpers	1	1_helper	−0.03	0.11	−0.25	0.19	−0.24	0.81
			treatment × n_helpers	1	2 + _helpers	0.06	0.14	−0.21	0.33	0.45	0.65
			treatment × n_helpers	2	0_helpers	−0.72	0.16	−1.03	−0.41	−4.52	<0.01
			treatment × n_helpers	2	1_helper	−0.35	0.14	−0.63	−0.07	−2.44	0.02
			treatment × n_helpers	2	2 + _helpers	0.00	0.00	0.00	0.00		
			blasttime			−0.05	0.03	−0.10	0.00	−1.95	0.05
			nestday			0.05	0.01	0.02	0.08	3.71	0.01
			est_hatchday			0.01	0.01	−0.01	0.02	1.80	0.07
			n_young			0.01	0.06	−0.11	0.13	0.19	0.85
arrivals	7	Nestling	intercept			0.06	0.89	−1.68	1.81	0.07	0.95
			treatment	1		0.28	0.09	0.10	0.46	3.05	0.01
			treatment	2		0.00	0.00	0.00	0.00		
			blasttime			−0.04	0.03	−0.09	0.01	−1.74	0.08
			nestday			−0.07	0.02	0.02	0.11	2.96	0.01
			est_hatchday			0.01	0.01	−0.01	0.02	0.97	0.33
			n_young			0.20	0.05	0.09	0.30	3.65	0.01
p_Onnest	1	Incubation	intercept			1.73	0.10	1.53	1.92	17.28	<0.01
		Nestling	intercept			1.09	0.12	0.86	1.33	9.00	<0.01

Table 12. Analyses of generalized estimating equation (GEE) parameter estimates and associated empirical standard error (SE) estimates for models at a 60-min time frame based on data from red-cockaded woodpecker nests on Fort Stewart, Georgia, 1999–2000. We modeled no. of arrivals using Poisson regression and p_onnest using logistic regression. Normal deviate statistic *Z* and associated *P*-values test the difference of the parameter from zero. See Table 2 for definitions of variables.

Dependent variable	Model no.	Nest phase	Parameter	Level 1	Level 2	Estimate	SE	95% CI Lower	95% CI Upper	*Z*	*P*-value
arrivals	14	Incubation	intercept			1.14	0.17	0.80	1.48	6.57	<0.01
			treatment × stimulus	1	Artillery	0.49	0.15	0.20	0.78	3.29	0.01
			treatment × stimulus	1	Blank	0.50	0.10	0.30	0.69	4.97	<0.01
			treatment × stimulus	2	Artillery	0.30	0.16	−0.02	0.61	1.83	0.07
			treatment × stimulus	2	Blank	0.00	0.00	0.00	0.00		
			n_helpers	0_helpers		−0.27	0.18	−0.62	0.08	−1.50	0.13
			n_helpers	1_helper		0.04	0.16	−0.28	0.35	0.21	0.83
			n_helpers	2 + _helpers		0.00	0.00	0.00	0.00		
			nestday			0.03	0.02	−0.01	0.07	1.63	0.10
arrivals	10	Nestling	intercept			1.32	0.13	1.07	1.57	10.34	<0.00
			treatment	1		0.22	0.11	0.01	0.43	2.03	0.04
			treatment	2		0.00	0.00	0.00	0.00		
			n_helpers	0_helpers		−0.26	0.09	−0.43	−0.08	−2.87	0.01
			n_helpers	1_helper		0.14	0.12	−0.09	0.37	1.20	0.23
		Nestling	n_helpers	2 + _helpers		0.00	0.00	0.00	0.00		
			nestday			0.16	0.03	0.10	0.21	5.58	<0.01
p_Onnest	1	Incubation	intercept			1.98	0.11	1.76	2.20	17.91	<0.01
	34		intercept			2.32	0.78	0.79	3.85	2.97	0.01
			lndistm			−0.12	0.19	−0.49	0.25	−0.62	0.53
			nestday			−0.03	0.05	−0.14	0.07	−0.63	0.53

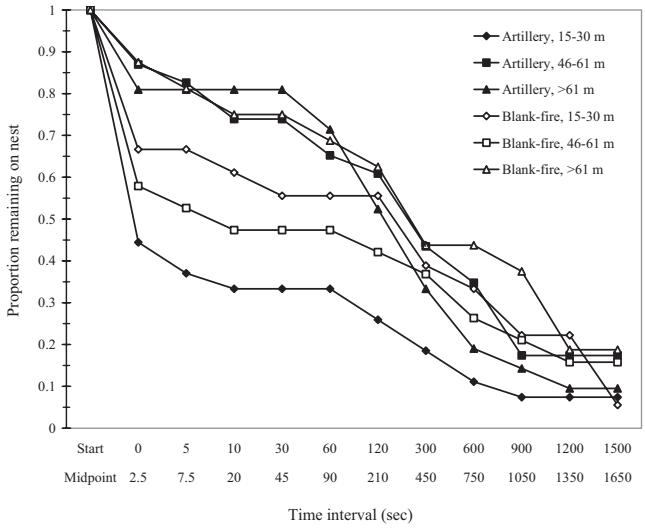

Figure 11. Life-table analysis of the flush response to military blast stimuli: incubation-stage nests of red-cockaded woodpeckers on Fort Stewart, Georgia, 1999–2000. The curves show the probability of a nesting bird remaining on the nest for various intervals after the stimulus event, for 2 stimulus types (artillery and blank fire). We considered flush times >30 min censored values for data with 30-min observation trials and uncensored for data with 60-min observation intervals.

flush responses to nonexperimental small-arms live fire at documented noise levels and stimulus distances. Woodpeckers did not flush from the nest when small-arms live fire events were >400 m from active woodpecker nests and SEL noise levels were <51 dBW (76 dB, unweighted; Table 13).

Only one woodpecker group (cluster 103) monitored between 1998 and 2000 received small-caliber live fire noise at <400 m. Noise levels at cluster 103 were louder than in other clusters due to supersonic bullet noise in close proximity to the nest tree (Fig. 14: example of noise spectral data). The other 13 clusters monitored for nonexperimental small-caliber noise were farther downrange than cluster 103 or were positioned behind the firing

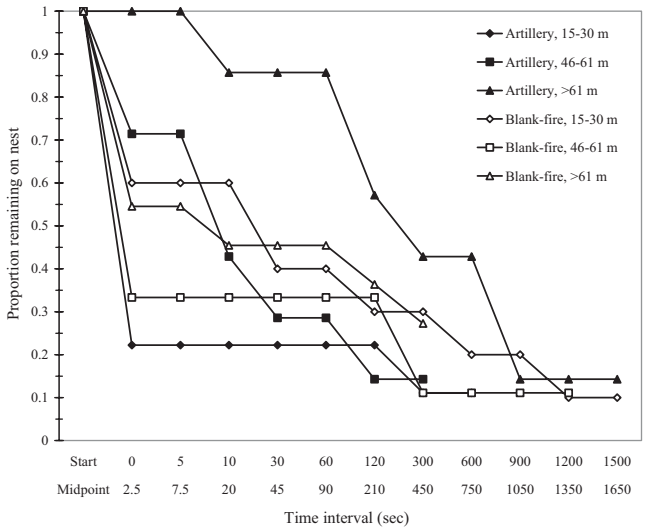

Figure 12. Life-table analysis of the flush response to military blast stimuli: nestling-stage nests of red-cockaded woodpeckers on Fort Stewart, Georgia, 1999–2000. The curves show the probability of a nesting bird remaining on the nest for various intervals after the stimulus event, for 2 stimulus types (artillery and blank fire). We considered flush times >30 min censored values for data with 30-min observation trials and uncensored for data with 60-min observation intervals.

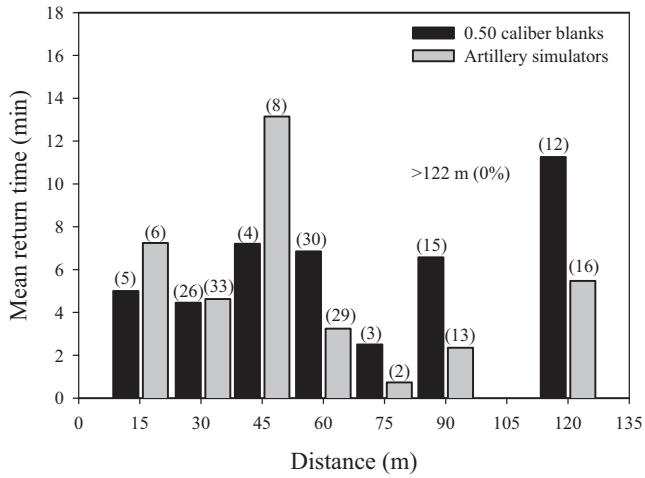

Figure 13. Mean return time for woodpeckers in response to experimental testing during 1999 through 2000 on Fort Stewart, Georgia. Gray bars represent data from artillery simulators, whereas black bars represent data from 0.50-caliber blank-fire tests. Values within parentheses represent the sample size tested at each distance.

lines and therefore received substantially lower noise levels (Table 13). We remotely monitored woodpeckers downrange from live-fire ranges via video cameras that we synchronized with audio recording equipment, although access to these sites was restricted to infrequent early morning periods during the course of this study.

We separated noise events into bullet noise (i.e., sonic booms generated by supersonic motion of bullets <200 m from the nest tree) or muzzle blast (i.e., noise from machine guns at the firing range approx. 430 m away) categories. We quantified each small-caliber noise event in terms of unweighted and dBW metrics (Fig. 15). Bullet noise was 20 to 25 dBW louder than muzzle blast noise within the 1- to 4-kHz frequency range when we compared peak levels for both noise types (Fig. 14). Supersonic bullet noise (i.e., a loud cracking sound) represented about 19% (284 noise events; Table 13) of noise events recorded at cluster 103. Cluster 103 successfully fledged 2 young each year that we monitored nesting success (1999–2000). Woodpeckers did not appear to flush in response to small-caliber noise at cluster 103, although their flight activities may have been influenced. On 3 days over a 6-day period in 1999, we observed woodpeckers arriving and departing from the nest only during inactive firing periods on the range.

Large-caliber live fire.—We recorded 630 large-caliber blasts or impacts during 45 data sessions at 24 woodpecker groups during 1998 through 2000 (Table 14; Delaney et al. 2002, Appendix D). Woodpeckers did not flush when large-caliber guns were fired at distances of >700 m from nests and SEL noise levels were <59 dBW (102 dB, unweighted; Table 14). Woodpeckers flushed in response to large-caliber blasts between 500 and 600 m from nests (1998). We did not record any large-caliber gun fire <500 m from any active woodpecker nest site; therefore, we could not test for response within that range.

Woodpeckers flushed twice in response to large-caliber (>20 mm) blast noise in 1998 through 2000. Both flush responses occurred at cluster 83 close to artillery blast noise events. This site received the highest nonexperimental noise levels of any woodpecker group we monitored. On 20 May

Table 13. Number, distance, and noise level of nonexperimental M-16 machine gun live-fire events recorded at active red-cockaded woodpecker (W) nests during 1998 through 2000 on Fort Stewart, Georgia.

				Noise levels (SEL [dB])[a]		
Distance (m)	Noise events	Data sessions	No. of flushes	Unweighted	W-weighted	Ambient LEQ[b] (dB), W-weighted
200–300	284	6	0	76–96	75–89	34–43
400–600	1128	8	0	58–77	43–75	34–41
800–900	29	1	0	67	47–51	34
1,200–2,500	313	7	0	64–72	34–62	32–35
4,000–5,000	171	6	0	62–76	33–47	30–34
5,001–7,000	5	1	0	75–76	27–30	23–25
Totals	1930	29	0			

[a] SEL = sound-exposure level; dB = decibels.
[b] Average noise level.

Table 14. Number, distance, and noise level of nonexperimental large-caliber (>20 mm) live-fire events recorded at active red-cockaded woodpecker (W) nests during 1998 through 2000 on Fort Stewart, Georgia.

				Noise levels (SEL [dB])[a]		
Distance (m)	Noise events	Data sessions	No. of flushes	Unweighted	W-weighted	Ambient LEQ[b] (dB), W-weighted
500–600	73	2	2	98–108	64–86	33–41
700–800	2	1	0	102–103	70–75	30
1,000–3,000	284	14	0	69–103	39–61	28–35
3,001–5,000	168	14	0	60–96	36–61	20–33
5,001–7,000	11	5	0	59–86	30–42	28–31
7,001–9,000	72	3	0	72–84	26–31	22–25
9,001–11,000	20	6	0	66	27–30	20–25
Totals	630	45	2			

[a] SEL = sound-exposure level; dB = decibels.
[b] Average noise level.

Table 15. Number, distance, and noise level of nonexperimental helicopters recorded at active red-cockaded woodpecker (W) nests during 1998 through 2000 on Fort Stewart, Georgia.

				Noise levels (SEL [dB])[a]		
Distance (m)	Noise events	Data sessions	No. of flushes	Unweighted	W-weighted	Ambient LEQ[b] (dB), W-weighted
30–50	11	5	0	103–110	84–92	33–35
51–100	11	5	0	96–101	79–84	33–37
101–200	21	12	0	90–104	68–81	23–37
201–300	25	16	0	87–99	61–74	31–36
301–500	15	7	0	73–85	40–64	25–34
Totals	83	45	0			

[a] SEL = sound-exposure level; dB = decibels.
[b] Average noise level.

Table 16. Number, distance, and noise level of nonexperimental military/civilian vehicles recorded at active red-cockaded woodpecker (W) nests during 1998 through 2000 on Fort Stewart, Georgia.

				Noise levels (SEL [dB])[a]		
Distance (m)	Noise events	Data sessions	No. of flushes	Unweighted	W-weighted	Ambient LEQ[b] (dB), W-weighted
15–50	58	13	2	58–110	56–91	33–35
51–100	12	2	0	82–99	58–73	33–37
101–200	5	2	0	72–93	64–75	23–37
201–300	2	2	0	84–87	49–52	31–36
301–500	4	3	0	76–79	43–54	25–34
Totals	81	22	2			

[a] SEL = sound-exposure level; dB = decibels.
[b] Average noise level.

Table 17. Number, distance, and noise level of nonexperimental missiles recorded at active red-cockaded woodpecker (W) nests during 1998 through 2000 on Fort Stewart, Georgia.

				Noise levels (SEL [dB])[a]		
Distance (m)	Noise events	Data sessions	No. of flushes	Unweighted	W-weighted	Ambient LEQ[b] (dB), W-weighted
750–1,000	33	2	0	67–105	25–85	22–24
2,000–4,000	62	3	0	65–93	39–64	30–32
4,001–6,000	18	2	0	58–85	32–53	27–31
Totals	113	7	0			

[a] SEL = sound-exposure level; dB = decibels.
[b] Average noise level.

Table 18. Number, distance, and noise level of nonexperimental simulator blasts recorded at active red-cockaded woodpecker (W) nests during 1998 through 2000 on Fort Stewart, Georgia.

				Noise levels (SEL [dB])[a]		
Distance (m)	Noise events	Data sessions	No. of flushes	Unweighted	W-weighted	Ambient LEQ[b] (dB), W-weighted
100–200	2	2	1	92–95	78–84	35–38
300–400	6	6	0	80–83	47–61	44–45
Totals	8	8	1			

[a] SEL = sound-exposure level; dB = decibels.
[b] Average noise level.

1998, we recorded 13 artillery blasts (155-mm rounds) during 1 data session at cluster 83. The attending adult appeared to flush from the nest in response to the loudest blast event recorded during that data session (seventh of 13 blast events recorded; SEL = 77 dBW [108 dB, unweighted]). The woodpecker returned to the nest after 6.25 minutes and did not flush in response to a subsequent blast of approximately equal noise level. On 21 May 1998, we recorded 60 artillery blast events during another data session at cluster 83. The attending adult appeared to flush in response to the 52nd blast event during that data session, returning to the nest after 4.42 minutes shortly before the last noise event recorded occurred during that data session. Blast event number 52 was one of the louder blasts of the day, with an SEL noise level of 79 dBW (105 dB, unweighted). Cluster 83 did not fledge young during any year of our study.

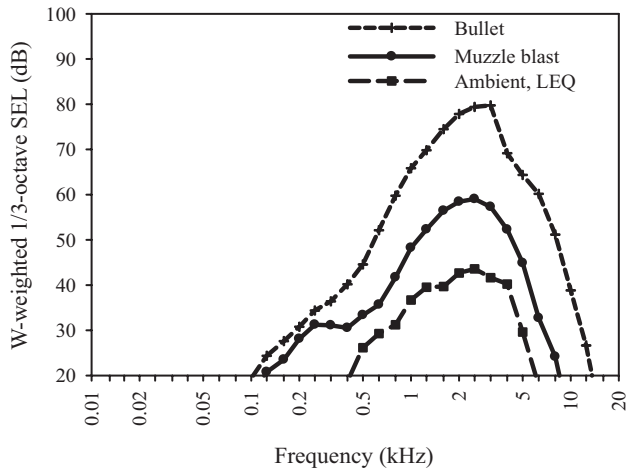

Figure 14. Example of a frequency spectrum for M-16 machine gun bullet noise, muzzle blast noise, and ambient sound recorded near red-cockaded woodpecker cluster 103 on Fort Stewart, Georgia, 13 May 1999. dB = decibels; LEQ = average noise level; SEL = sound-exposure level.

Helicopters.—We recorded 83 helicopter passes during 45 data sessions at 19 woodpecker groups during 1998 through 2000 (Table 15). We recorded more than twice the number of helicopter events and data sessions during the 2000 field season than during 1998 and 1999 combined due to increased helicopter

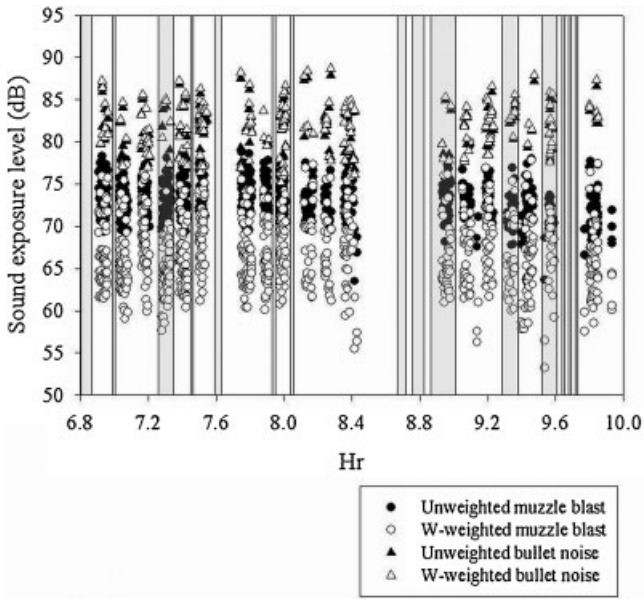

Figure 15. Sound exposure level–weighting comparison of sonic booms generated by supersonic motion of nonexperimental small-arms live fire approximately 200 m and from muzzle blast noise approximately 440 m from M-16 rifles near active red-cockaded woodpecker cluster 103 for 0700 to 1000 hours on Fort Stewart, Georgia, 6 May 2000. Nonshaded areas represent times when adult red-cockaded woodpeckers were attending the nest, whereas gray-shaded areas were times when adults were away from the nest. Events with equal woodpecker (W)–weighted and unweighted levels, or where W-weighted levels are higher than unweighted values, represent supersonic bullet noise (triangles with approximately 78 decibels [dB], unweighted or higher). Events with W-weighted levels below unweighted levels (circles <78 dB, unweighted) represent muzzle blast noise from the range.

training on the installation. We did not observe any flush responses by woodpeckers relative to documented noise levels and stimulus distances. Woodpeckers did not flush from nests during the incubation or early brooding phase when military helicopters were as close as 30 m to nests and SEL noise levels were <84 dBW (102 dB, unweighted; Table 15; Delaney et al. 2002, Appendix D).

Military and civilian vehicles.—We recorded 81 military and civilian vehicle passes during 22 data sessions at 15 woodpecker groups during 1998 through 2000 (Table 16). Woodpeckers flushed twice in response to vehicle noise during these data sessions. These flush events occurred at clusters 216 (1999) and 23 (2000) in response to a Bradley fighting vehicle convoy and a civilian vehicle, respectively. At cluster 216, a convoy of 17 Bradley fighting vehicles passed within 30 m of the nest tree, eliciting a flush response by the attending adult (Delaney et al. 2002, appendix D). A woodpecker returned to the nest in 10 minutes, after the convoy had passed. This site successfully fledged 1 young. The second flush occurred at cluster 23 as a civilian vehicle passed 15 m from the nest tree. A bird returned to the nest within 3 minutes after the flush. This site failed during this first nesting attempt, but successfully fledged 1 young during a second nesting attempt. Overall, woodpeckers did not flush when vehicles were >50 m from nests and SEL noise levels were <55 dBW (75 dB, unweighted; Table 16).

Missiles.—We only recorded woodpecker response to 1 multiple launch rocket system (MLRS) firing event at cluster 88 during the early brooding phase in 1999. This noise event did not elicit a flush response. All other missile recordings occurred before nest initiation or during the nestling phase when adult presence was not consistent to allow for response testing. Missile events at distances of <1,000 m represent MLRS noise events (Table 17; Delaney et al. 2002, Appendix D), whereas distances of >2,000 m represent Stinger missile noise events (Delaney et al. 2002, Appendix D). Red-cockaded woodpeckers did not flush when MLRSs were fired >750 m from nests and SEL noise levels were <25 dBW (69 dB, unweighted; Table 17). Due to the low probability of encountering missile fire, we were unable to test for woodpecker response at distances of <750 m.

Artillery and grenade simulators.—We recorded 8 nonexperimental simulator blasts during 8 data sessions at 2 woodpecker groups in 1998 and 1999 (Table 18). Woodpeckers flushed once in response to a nonexperimental grenade simulator blast about 30 m from a nest in 1999 during a realistic training maneuver (Delaney et al. 2002, Appendix D). A woodpecker returned to the nest within 8 minutes after the flush (this site successfully fledged 1 young). Overall, woodpeckers did not flush when grenade simulators were detonated >200 m from nest sites and SEL noise levels were <47 dBW (82 dB, unweighted; Table 18). We did not record any nonexperimental grenade simulator blasts >100 m from any active red-cockaded woodpecker nests; therefore, we could not test for response within this range.

Dose-Response Modeling of Flush Response

We used 98 artillery simulator blast events and 85 blank-fire events to determine dose-response curves for flush responses of red-cockaded woodpeckers from the nests from 1999 and 2000 (Table 19). The results are summarized in Table 20, which shows information-theoretic comparisons among logistic regression models of red-cockaded woodpecker flush response with respect to the 3 differently weighted stimulus dB levels, and the intercept-only (no stimulus effect) model. The parameter values for the logistic regression models in Table 20 are given in Table 21.

We found no support for a statistically detectable effect of blank-fire stimulus intensity on the flush response of red-cockaded woodpeckers (Table 20, stimulus = blank). The most parsimonious model was the constant response (intercept only) model in both 1999 and 2000. This was true whether stimulus intensity was measured by dBA, dBW, or dBF. In 1999, the intercept-only model was the most parsimonious model, although models including dBW, dBA, and dBF also had substantial support from the data ($\Delta AIC_c < 0.1$). In 2000, the intercept-only model was again the most parsimonious model. Models including dBW, dBA, and dBF had borderline-substantial support from the data, with $\Delta AIC_c \approx 1.9$ to 2.2.

On the other hand, the data provided substantial support for models in which artillery fire stimulus intensity increased the flush response of red-cockaded woodpeckers (Table 20, stimulus = artillery). This was true when intensity was measured by dBA (1999 and 2000) or by dBW (2000 only). In 1999, the data most strongly supported the models including dBW and dBA. The model including dBW was best, but the model including dBA also had strong support ($\Delta AIC_c \approx 0.07$). The intercept-only model and the model including dBF had equivocal or no support from the data ($\Delta AIC_c \approx 5$). In 2000, the data supported the model including dBA most strongly. Support for the second best supported model, that including dBW, was weak ($\Delta AIC_c \approx 3$) compared with the model including dBA. The model including dBF and the intercept-only model had little or no support from the data ($\Delta AIC_c > 7$).

The effect of artillery fire on the red-cockaded woodpecker flush response appeared to be somewhat stronger in 1999 than in 2000 (Figs. 16 and 17, derived from the corresponding models in

Table 19. Sample sizes for data used in determining dose-response curves for flush responses of red-cockaded woodpeckers from the nest in reaction to artillery simulators vs. 0.50-caliber blank fire during 1999 through 2000 on Fort Stewart, Georgia.

		Distance (m)									
Stimulus	**Year**	**15.2**	**30.5**	**45.7**	**61.0**	**76.2**	**91.4**	**121.9**	**152.4**	**243.8**	**Total**
Artillery	1999	3	16		16		3	9		1	48
	2000	3	15	7	11	2	6	5	1		50
Subtotal		6	31	7	27	2	9	14	1	1	98
Blank	1999	4	12		13		8	9			46
	2000	1	9	4	12	2	6	3	1	1	39
Subtotal		5	21	4	25	2	14	12	1	1	85
Total		11	52	11	52	4	23	26	2	2	183

Table 20. Information-theoretic rankings of logistic regression models of flush response with respect to 3 differently weighted functions in decibels (unweighted [dBF], human-based A-weighted [dBA], and woodpecker-weighted [dBW]) and the intercept-only (no stimulus effect) model for nesting red-cockaded woodpeckers on Fort Stewart, Georgia, 1999–2000. Only models with substantial support from the data (difference in the second-order Akaike Information Criterion for the model from the smallest such value in the set of candidate models [ΔAIC_c] ≤ 2) are shown. We performed analyses separately for data from each blast stimulus type and year of study. Terminology and methods are as given in Burnham and Anderson (2002).

Stimulus	Year	ΔAIC_c	w_AIC_c[a]	Model	Pearson χ^2	df	χ^2/df	K[b]
Artillery	1999	0.000	0.468	dBW	51.2	46	1.11	2
		0.070	0.452	dBA	50.7	46	1.10	2
		4.758	0.043	dBF	50.5	46	1.10	2
		5.094	0.037	Intercept	48.0	47	1.02	1
	2000	2.934	0.183	dBW	48.3	48	1.01	2
		0.000	0.793	dBA	47.2	48	0.98	2
		7.010	0.024	dBF	49.7	48	1.03	2
		16.380	0.000	Intercept	50.0	49	1.02	1
Blank	1999	0.475	0.238	dBW	47.1	45	1.05	2
		0.538	0.231	dBA	47.0	45	1.05	2
		0.561	0.228	dBF	47.0	45	1.04	2
		0.000	0.302	Intercept	47.0	46	1.02	1
	2000	2.229	0.159	dBW	37.0	35	1.06	2
		2.111	0.169	dBA	37.0	35	1.06	2
		1.905	0.187	dBF	37.0	35	1.06	2
		0.000	0.485	Intercept	37.0	36	1.03	1

[a] Corresponding Akaike weight for that model.
[b] No. of estimable parameters in the model.

Table 21). The stimulus level at which 50% of the birds flushed was 98 dB in 1999, versus 80 dB in 2000 using dBA weighting. The corresponding values were 92 dB in 1999 versus 73 dB in 2000 using dBW weighting.

DISCUSSION

It is important when examining human impacts on animals that disturbance sources be quantified and characterized during biologically important times for the subject animal of interest

Table 21. Parameter values for the candidate models used for information-theoretic rankings of logistic regression models of flush response with respect to 3 differently weighted functions in decibels (unweighted [dBF], human-based A-weighted [dBA], and woodpecker-weighted [dBW]) and the intercept (no stimulus effect) model for nesting red-cockaded woodpeckers on Fort Stewart, Georgia, 1999–2000.

								95% CI			
Model no.	Predictor variable	Stimulus	Year	Parameter	df	Estimate	SE	Lower	Upper	χ^2	Pr > χ^2
1	None	Artillery	1999	intercept	1	−0.887	0.318	−1.542	−0.287	7.81	0.005
			2000	intercept	1	0.160	0.284	−0.395	0.724	0.32	0.572
		Blank	1999	intercept	1	0.043	0.292	−0.532	0.620	0.02	0.884
			2000	intercept	1	0.272	0.332	−0.375	0.938	0.67	0.413
2	dBF	Artillery	1999	intercept dBF	1	−15.987	10.298	−38.920	2.431	2.41	0.121
					1	0.148	0.101	−0.033	0.371	2.17	0.141
			2000	intercept dBF	1	−10.380	3.535	−18.084	−4.009	8.62	0.003
					1	0.116	0.039	0.046	0.200	9.04	0.003
		Blank	1999	intercept dBF	1	−4.684	3.784	−12.454	2.577	1.53	0.216
					1	0.051	0.040	−0.027	0.134	1.57	0.211
			2000	intercept dBF	1	−3.193	6.042	−15.591	8.631	0.28	0.597
					1	0.037	0.065	−0.089	0.170	0.33	0.566
3	dBA	Artillery	1999	intercept dBA	1	−17.206	7.109	−33.226	−4.833	5.86	0.016
					1	0.175	0.076	0.043	0.345	5.39	0.020
			2000	intercept dBA	1	−20.290	6.005	−34.058	−9.928	11.42	0.001
					1	0.253	0.074	0.125	0.422	11.71	0.001
		Blank	1999	intercept dBA	1	−4.231	3.407	−11.257	2.291	1.54	0.214
					1	0.049	0.039	−0.025	0.130	1.58	0.209
			2000	intercept dBA	1	−1.558	5.135	−12.058	8.643	0.09	0.762
					1	0.021	0.058	−0.095	0.140	0.13	0.721
4	dBW	Artillery	1999	intercept dBW	1	−15.552	6.501	−30.289	−4.392	5.72	0.017
					1	0.170	0.074	0.041	0.338	5.22	0.022
			2000	intercept	1	−17.002	5.318	−28.984	−7.714	10.22	0.001
				dBW	1	0.233	0.072	0.107	0.395	10.45	0.001
4	dBW	Blank	1999	intercept dBW	1	−4.040	3.202	−10.665	−4.392	1.59	0.207
		Blank	1999		1	0.050	0.039	−0.025	0.338	1.64	0.201
			2000	intercept dBW	1	−0.166	4.452	−9.148	−7.714	0.00	0.970
					1	0.005	0.054	−0.104	0.395	0.01	0.922

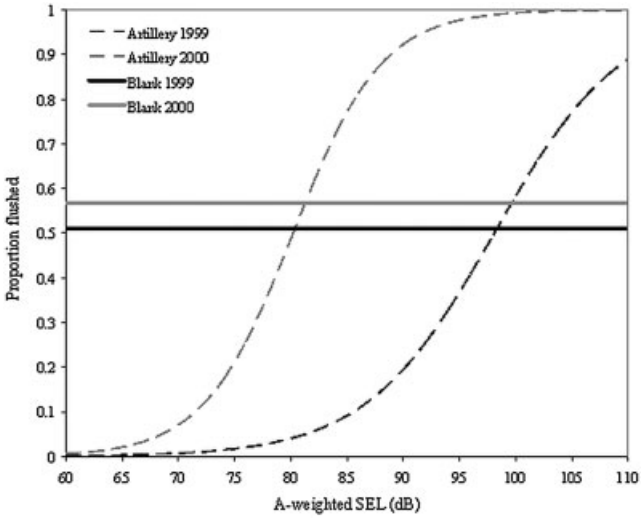

Figure 16. Flush response as a function of artillery fire stimulus intensity, with intensity measured by human-based weighted (A-weighted) sound-exposure levels (SEL), for nesting red-cockaded woodpeckers on Fort Stewart, Georgia, 1999–2000. The curves represent predicted values from logistic models back-transformed to proportions of birds flushing the nest. The average proportions of woodpeckers flushing the nest were unaffected by blank-fire during those years, and are shown as constant horizontal lines for comparison. dB = decibels.

(Delaney et al. 1999). For birds, one of these times is the nesting season, especially during courtship, incubation, and early in the brooding phase when adults are attending nests at much higher levels than later in the nestling phase. Few studies have attempted to quantify and characterize military training activities (Hayden et al. 2002) and noise (Doresky et al. 2001) in proximity to red-cockaded woodpecker groups. Most disturbance studies place their research sites within treatment and control sites based on anticipated training levels or restriction categories (J. Mobley, unpublished report; J. R. Walters, unpublished data; Perkins 2006) but have not monitored disturbance levels to confirm how representative they are of what animals are actually receiving. Designations between treatment and control sites can become blurred and overall research findings may be limited if researchers do not characterize differences in disturbance levels between treatment and control sites (Doresky et al. 2001, Perkins 2006).

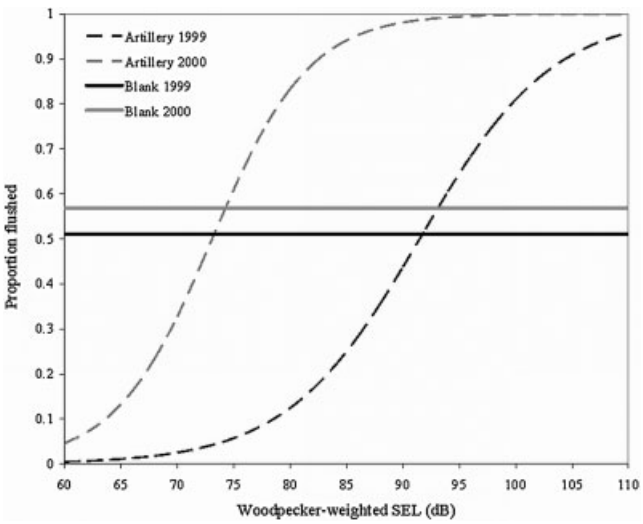

Figure 17. Flush response as a function of artillery fire stimulus intensity, with intensity measured by woodpecker-weighted sound exposure levels (SEL), for nesting red-cockaded woodpeckers on Fort Stewart, Georgia, 1999–2000. The curves represent predicted values from logistic models back-transformed to proportions of birds flushing the nest. The average proportions of woodpeckers flushing the nest were unaffected by blank fire during those years and are shown as constant horizontal lines for comparison.

We are not aware of other studies of disturbance of red-cockaded woodpecker that have experimentally controlled stimulus events, used frequency-weighting algorithms to relate sound levels to how woodpeckers perceive military training events, compared weighting functions and empirical data, or recorded both sound levels and frequency spectra to quantify and characterize noise sources. Without frequency spectra, it is not possible to understand how sound energy is distributed across the potential frequency range or to determine possible overlaps between bird hearing sensitivity and noise events. Few studies have tested the response of animals to anthropogenic disturbances over a range of controlled distances to develop dose-threshold relationships (Delaney et al. 1999). Experimental field tests provide a number of benefits over nonexperimental disturbance testing.

Reproductive Measures

Military training events on Fort Stewart did not affect red-cockaded woodpecker reproduction based on the level (i.e., stimulus distance, noise level, timing, duration, group size, and frequency of noise events) or type of anthropogenic noise sources tested (weapons fire, helicopter and aircraft overflight, and vehicle maneuvers). Experimental sites did not differ from control sites in number of eggs, nestlings, or fledglings produced. Other researchers similarly have reported no difference between treatment and control groups for red-cockaded woodpeckers relative to military training activities (Doresky et al. 2001, Hayden et al. 2002), whereas other studies have been either inconclusive (J. R. Walters, unpublished data) or have reported some reduction in measures of reproduction (J. Mobley, unpublished data; Perkins 2006). We believe the small but nonsignificant decrease in reproductive measures between treatment and control woodpecker groups suggests that demonstration of behavioral responses at one level, such as flush frequency and nest arrivals, does not necessarily equate to impacts at a higher, more biologically important level, such as reproduction. We suggest that the cooperative breeding system of red-cockaded woodpeckers (i.e., helpers) helps compensate for natural and human-based disturbance events by buffering potential reductions in parameters associated with nesting, such as nest attendance and prey delivery rates.

There is no clear consensus on how anthropogenic disturbances may impact red-cockaded woodpecker populations. Perkins (2006) noted an increase in partial brood loss within control nest sites that limited military training activities compared with experimental nests that did not limit military training operations, although this result was not consistent among years. Reductions in other demographic measures were not observed (Perkins (2006). Perkins (2006) suggested that the observed variation in partial brood loss was likely influenced by data from 2002.

Partial brood loss was substantially higher in 2002 at control sites and substantially lower at experimental sites compared with the average. When 2002 data were removed from the analyses, there was no difference between treatments, which Perkins (2006) suggested may have been due to habituation and the impact from military training operations, but no empirical data were provided for this assertion.

Human presence has a greater impact on animal behavior versus disturbances without a visible human component, such as from external noise sources, aircraft, or vehicles (Jackson 1983, Delaney et al. 1999). J. Mobley (unpublished data) observed reductions in nesting success, number of fledglings, and clutch size and increased male breeder turnover for clusters close to landing zones and bivouac sites. We believe differences between our results and Mobley are partially due to the type and duration of military sources tested. Mobley tested the effects of extended human presence on woodpecker reproductive parameters, whereas our experimental trials tested short-duration military training exercises and associated noise with limited human presence. Available literature does not provide a clear link between short-term response measures for animals (e.g., flush response) and long-term impacts on animal reproduction unless a disturbance source is close, such as an approaching human (i.e., surrogate for a potential nest predator; Frid and Dill 2002).

Hearing

No studies have addressed hearing sensitivity of red-cockaded woodpeckers directly. Our project is the first to have studied hearing sensitivity of downy woodpeckers as surrogates for red-cockaded woodpeckers, although downy woodpecker hearing sensitivity has been evaluated in comparison to passerines (Lucas et al. 2002). The general similarity in characteristics of the vocal spectra of downy woodpeckers and red-cockaded woodpeckers, in addition to their close taxonomic relationship, suggests that hearing abilities of the 2 species should be similar. In addition, the best sensitivity of the downy woodpecker ABR thresholds corresponds to the peak in the power spectrum of both downy and red-cockaded woodpecker vocalizations. Thus, it appears that the downy woodpecker serves as a good model for hearing in the red-cockaded woodpecker. Extrapolating from what is known about human equal-loudness curves, it is likely that our woodpecker-weighting curve attenuated the sound somewhat more than is ideally appropriate at high and low frequencies for moderate sound stimulus levels, but this seemed preferable to making unsubstantiated assumptions regarding how much to reduce the attenuation at high and low frequencies. Further research is needed and, indeed, is of substantial current interest within the acoustical scientific community.

We observed some variability in data across downy woodpeckers, suggesting that further testing with a larger sample is warranted. It appears that the shape of the woodpecker audiogram was broadly comparable to that of small passerine birds but showed a greater sensitivity at higher frequencies compared to the average passerine (frequency of best sensitivity is higher). Behavioral thresholds for budgerigars are typically 50 dB to 60 dB higher at this frequency than at their best frequency (approx. 2,860 Hz), possibly accounting for the lack of response with the generally less sensitive ABR method of estimating hearing thresholds. More research is needed to further test woodpecker hearing sensitivity at frequencies of <0.5 kHz. The best sensitivity of the downy woodpecker ABR thresholds is at a somewhat higher frequency than that for a typical passerine. In contrast, Lucas et al. (2002) found that downy woodpeckers were weaker in high-frequency sensitivity than various passerine species, although this may be due to differences in testing procedures (i.e., variation in click intensity, duration, and periodicity) or seasonal variation in hearing sensitivity (Lucas et al. 2002). Birds with simpler vocal patterns, such as woodpeckers, showed a greater amplitude response to clicks and had a shorter latency (i.e., time delay between the moment woodpeckers were presented with clicks and when clicks were detected by woodpeckers) in winter than in spring (Lucas et al. 2002). Data also suggested that the auditory system for woodpeckers may be correlated with vocal complexity (Lucas et al. 2002). Overall, woodpeckers may have a reduced auditory sensitivity relative to other species of small birds, especially in the higher-frequency range (Dooling et al. 2000, Lucas et al. 2002). Given the similarity in spectral structure of the vocalizations of small woodpeckers, auditory sensitivity is probably similar in the downy woodpecker and other *Picoides* species such as the red-cockaded woodpecker. More research is needed to further test red-cockaded woodpeckers' hearing sensitivity, especially at frequencies of <0.5 kHz.

What might account for the higher threshold at best frequency for downy woodpeckers compared with small passerines? One potential explanation emerges from the technique of measuring evoked potentials at the surface of the skull. The skull is thicker in woodpeckers than in budgerigars or small passerines. An increased skull thickness and other adaptations with woodpecker ear anatomy and musculature is likely a protective adaptation for drumming and other percussive behaviors in woodpeckers (Spring 1965; May et al. 1976, 1979; Gibson 2006). It remains to be determined whether such adaptations also include a reduction in auditory sensitivity compared with other small birds or whether skull thickness (or other active hearing-protective mechanisms in the woodpecker ear) prevents measurement of true tone thresholds using the ABR technique. As more individual birds and species are tested, researchers will be more confident in their assessments of the actual thresholds involved for small woodpeckers and their relationship to thresholds already determined for other species of small birds.

Noise Monitoring

Few researchers have directly compared differences in bird responsiveness between aerial and ground-based disturbances (Bowles et al. 1990). Studies that have examined effects of aircraft activity on nesting birds (e.g., J. Windsor, Canadian Wildlife Service, unpublished data; Platt 1977; Anderson et al. 1989; Delaney et al. 1999) have often noted a slight but statistically insignificant decrease in nesting success and productivity for experimental versus control nests. In contrast, ground-based disturbances appear to have a greater effect than aerial disturbances on nesting success of some bird species, possibly due to a more direct association with human presence (Jackson 1983, Delaney et al. 1999).

A bird's behavior during the nesting season is an important determinant of its ultimate nesting success or failure (Hohman

1986). Various bird species have been reported to abandon their nests after being exposed to ground-based and aerial disturbances. Birds may be more susceptible to disturbance-caused nest abandonment early in the nesting season, possibly because parents have less energy invested in the nesting process (Knight and Temple 1986), although there does not appear to be a consensus on why birds abandon nests earlier in the nesting season. Although reactions of adult birds at the nest to human disturbances can influence hatching rates and fledging success, flush behavior of adult birds from the nest is poorly quantified (Windsor 1977, Fraser et al. 1985, Holthuijzen et al. 1990, Delaney et al. 1999). In the few studies that examined bird responses to specific disturbance types (e.g., aircraft approach distance), flush rates were higher if birds were naive (Platt 1977). Some birds are more reluctant to flush off the nest during incubation and early nestling phases than later in the season (Grubb and Bowerman 1997, Delaney et al. 1999). Animal responsiveness increases as the nesting season progresses (Grubb and Bowerman 1997, Delaney et al. 1999).

Red-cockaded woodpeckers in our study received a wide range of noise levels at a given distance. Different types of noise sources emit different acoustic source energy. Noise sources can vary in number of noise events that occur within a specific period (i.e., 1 round from a 0.50-caliber machine gun vs. a 10-round burst). Noise sources also can vary depending on how they were manufactured (e.g., amount of explosive power in an artillery simulator). Researchers observed a difference in emissive power for the same type of military-issued artillery simulators (at similar distances) during experimental testing between 1999 and 2000 (Delaney et al. 2002), although this did not translate into any detectable variation in woodpecker flush response between years.

The received noise level for a given noise source also depends on differences in propagation conditions, a result of differences in atmospheric wind and temperature structure (Piercy et al. 1977, Embleton 1982, White and Gilbert 1989, Larsson and Israelsson 1991, Li et al. 1994). At distances of several kilometers, received noise levels can vary by as much as 50 dB due to changes in meteorological conditions (White et al. 1993). Differences in received noise level also can be due to orientation of the weapon relative to the receiver; many guns exhibit substantial directivity varying by as much as 15 dB louder downrange versus behind the gun (Pater 1981).

Behavioral responses of red-cockaded woodpeckers varied depending on the nesting phase and type of nesting activity. We found no treatment or stimulus effects on nest attendance during the incubation and early brooding phase when adults were present at the nest for extended periods. Woodpeckers exhibited the strongest response to experimental testing within the first 5 seconds of stimulus events. During both nesting phases, we observed the most pronounced flush effects when artillery simulators were at close range and blank-fire events were at close or medium distances from woodpeckers. In summary, the proportion of woodpeckers that flushed in response to experimental training noise was negatively related to stimulus distance and positively related to noise level. Similar patterns have been reported for other bird genera (Grubb and King 1991, McGarigal et al. 1991, Delaney et al. 1999) but not previously for any woodpecker species.

It is important to consider all aspects, including visual impacts, of stimulus events when examining animal response to a disturbance. There were inherent differences in how 0.50-caliber and artillery simulators were presented to woodpeckers during field tests according to how the military trains. Artillery simulator blasts were much shorter in duration and required fewer personnel to detonate than blank-fire training events, which lasted substantially longer. Our data indicated that red-cockaded woodpeckers flushed more rapidly in response to 0.50-caliber blank-fire events than artillery simulators at distances of 46 to 61 m for both nesting and fledgling stage nests (Figs. 11 and 12) and beyond 61 m for nestling stage nests (Fig. 12). However, at 15 m to 30 m artillery simulators tended to elicit faster flush responses than blank fire (Figs. 11 and 12). The visibility of the noise source, frequency of occurrence, and duration of the noise stimuli may explain these trends. At closer distances to a woodpecker's location (<45 m), we propose that a disturbance may be highly visible to attending adult woodpeckers from the mouth of the nest cavity and therefore may elicit a greater response than a disturbance farther away, regardless of noise level. On the other hand, the longer temporal scale and greater human presence associated with the blank-fire events may have led to the more rapid flushing of birds at distances beyond 45 m. Woodpeckers returned to their nests quickly after being flushed, regardless of whether military events were nonexperimental or experimentally controlled. Return times by woodpeckers were comparable to return times to nests reported for bird species in other noise disturbance studies (Awbrey and Bowles 1990, Holthuijzen et al. 1990).

Time that an attending adult is away from the nest has important consequences for nesting success due to potential impacts of nest depredation and nest kleptoparasitism on red-cockaded woodpeckers. Rat snakes (*Elaphe alleghaniensis*) frequently prey on cavity-nesting birds and can depredate red-cockaded woodpecker eggs and nestlings (Jackson 1970, 1974, 1978; Neal et al. 1993; Delaney et al. 2008), but in lower numbers than other species of cavity-nesting birds (e.g., Hensley and Smith 1986, Eichholz and Koenig 1992), primarily due to the effectiveness of the resin barrier that red-cockaded woodpeckers create through regular resin well maintenance (Rudolph et al. 1990*b*). Several species are capable of usurping nesting cavities from red-cockaded woodpeckers, including red-bellied (*Melanerpes carolinus;* Kappes 1997, Delaney and Carlile 2010) and red-headed woodpeckers (*M. erythrocephalus;* Jackson 1994), which can remove eggs or young while usurping the cavity. Southern flying squirrels (*Glaucomys volans*) also eat red-cockaded woodpecker eggs while usurping nest cavities (Harlow and Doyle 1990), although there is disagreement over whether cavity kleptoparasitism by flying squirrels substantially reduces red-cockaded woodpecker reproduction (USFWS 2003). Some researchers suggest that cavity kleptoparasitism by flying squirrels reduces nesting attempts by red-cockaded woodpeckers (Loeb and Hooper 1997), whereas others researchers reported no impact by flying squirrels on nesting attempts (Mitchell et al. 1999). It does not appear that nest depredation or cavity kleptoparasitism has an impact on red-cockaded woodpecker nesting success on Fort Stewart, based on the few documented cases on the installation during 1998 through 2000 (Delaney et al. 2008).

Distance and Sound Thresholds

Few studies have documented the threshold distance that causes birds to flush in response to noise disturbances. In studies that reported stimulus distance, it was rare for birds to flush when the stimulus distance was >60 m (R. G. Edwards, U.S. Department of Transportation, unpublished data; Carrier and Melquist 1976, Craig and Craig 1984, Delaney et al. 1999). Many disturbance studies report that animal response increases with decreasing stimulus distance (Platt 1977, Grubb and King 1991, McGarigal et al. 1991, Stalmaster and Kaiser 1997), although only a few studies have experimentally tested this relationship (Delaney et al. 1999). Even fewer examples exist for dose-response relations where models are still in development (Bowles 1995). Snail kites (*Rostrhamus sociabilis*) did not flush even when noise levels were up to 105 dB (A-weighted) from commercial jet traffic; however, test birds were living near airports and may have habituated to the noise (N. F. R. Snyder, Florida Audubon Society, unpublished data). R. G. Edwards (unpublished data) found a dose-response threshold of approximately 95 dBA for flush responses when approach distances were between 30 and 60 m.

We addressed noise-event distances and sound thresholds on a case-by-case basis as recommended by Delaney et al. (1999) due to variation in noise level and frequency spectra for nonexperimental noise sources on Fort Stewart. It is unlikely that most woodpeckers would receive as much disturbance activity during the nesting season as the experimental groups received during any single year for our study because of the varied nature and location of maneuver training operations on Fort Stewart, which is supported by Hayden et al. (2002), who reported that few red-cockaded woodpecker groups experienced high levels of military maneuver training operations on Fort Stewart. Despite the aggressive nature of our testing regime (i.e., close proximity and repeated exposure), woodpecker behavioral responses were minimal when experimental stimuli were >121.9 m away, and birds did not flush from the nest when noise sources were >152.4 m away. Even when we performed more aggressive noise tests (≤91.4 m from a woodpecker's position), woodpeckers returned to their nests quickly after being flushed and did not abandon their nests or suffer a reduction in reproduction compared with control woodpecker groups. In addition, life-table analyses on flush time showed that most differences in flush time among stimuli and distance classes appeared within 5 seconds of the blast stimuli.

Effects of Blast Stimuli on Woodpecker Nesting Behavior

We observed fewer woodpecker arrivals to the nest after stimulus events than before stimulus events during incubation and nestling phases. Adult caretakers responded to disturbance by spending longer average bouts (i.e., more time) on the nest, at the cost of reducing the feeding rate after the blast, which could lead to reduced nest-attendance rates if stimulus events occur over extended periods or over multiple days during the incubation period, as evidenced in J. Mobley (unpublished data). If disturbance events are infrequent, bird behavior can return to the before-disturbance condition quickly, as seen in other bird species (Delaney et al. 1999).

Our analyses supported an overall beneficial effect of helpers on the response of woodpecker arrival rates to disturbance. Data from incubation-phase nests at the 30-minute time frame supported the hypothesis that helpers can mitigate the effect of blast treatments on arrival rates. We detected no such mitigating effect of helpers for nests in the nestling phase. The lack of an effect in the nestling phase could result from reduced statistical power, due to smaller samples for the nestling phase. Helpers are known to assist with nest attendance and provisioning nestlings and may buffer potential reductions in these variables due to human disturbances (Walters et al. 1988, Conner et al. 2001, Khan and Walters et al. 2002), although this needs to be investigated in more detail.

Distance may have 2 confounding effects. It might affect behavior at the nest through 2 causal paths: 1) attenuation of blast dB levels with distance and 2) direct effects of experimenter presence at different distances. Distance effects in general were not apparent among the models with substantial support in our experiment, although the effect of blast treatments might be expected to decrease over distance. In particular, we might expect a distance effect to be present in treatment 2 (postimpulse) but not in treatment 1 (preimpulse), producing a treatment × ldistance interaction. The only model with support that included distance as a factor in our results was p_onnest in the incubation phase at the 60-minute time frame. The parameter for this effect was negative in sign but did not statistically differ from zero. It is not clear from our results whether the range of distances used was not great enough to produce a statistical effect for distance or if sample sizes were simply not adequate to detect distance effects in our study.

Variables used as covariates in these analyses were not of primary concern, being used mainly as statistical controls (Milliken and Johnson 2002, Morrison et al. 2008). For arrival rates, the signs of parameters for covariate effects seen in these models generally agreed with what might be expected a priori. Effects of nestday were generally positive in sign for both the incubation phase (indicating an increase in arrivals as hatch day approached) and the nestling phase (indicating an increase in arrivals with number of days after hatch, presumably reflecting increased feeding rates as nestlings grew in size). The parameter for number of young (n_young) in the nest was positive for the nestling phase but close to zero for the incubation phase, which one might expect if arrivals correlate with feedings of nestlings as they grow. The variable blasttime had negative parameter values, which we expect if overall activity at the nest decreases from early morning to early afternoon (D. Delaney, U.S. Army Construction Engineering Research Laboratory, unpublished data). The variable est_hatchday had positive parameter values, suggesting an overall tendency for nests started later in the season to show higher arrival rates than those started earlier in the season, perhaps reflecting increases in abundance of insect prey (and therefore prey delivery rates) as the breeding season progresses. Because these covariates had some effects statistically different from zero, statistical control for these variables seems advisable for future studies of this sort when sample sizes permit their inclusion (Nelder and Wedderburn 1972).

Little evidence supports that W-weighting is a better predictor than A-weighting of woodpecker flush response based on our

sample sizes and level of testing, but more testing is warranted. Results varied among years for artillery fire. Artillery blasts may have been effective drivers of flush behavior only at shorter distances from the nest, whereas blank fire may have elicited flushes more equally effectively over longer distances from the nest. This hypothesis is weakened by the lack of substantially supported models with distance or stimulus $\times$ distance effects in the nesting behavior study. Our initial examination into the dose-response relationship between woodpecker flush frequency and SPL does not provide a strong answer as to which weighting function is a better predictor of woodpecker response, and we believe that more testing is warranted. It is important that woodpecker response be compared against other stimulus dose measures using larger sample populations if possible. Regardless of these initial dose-response findings, we believe that the W-weighting function we developed may provide a realistic perspective of how woodpeckers perceive sounds within their environment.

Benefits of Land Management Practices

We believe that land management practices play a more important role in the overall success, growth, and sustainability of red-cockaded woodpecker populations on military lands than maneuver training operations or noise. Fort Stewart, as with other DoD installations, has made substantial strides in improving red-cockaded woodpecker habitat quality on their lands (Britcher and Patten 2005, Carlile et al. 2005, Costa 2005). Land management practices, such as frequent prescribed-burning rotations, hardwood control, commercial thinning, reestablishment of native ground cover, conservation and regeneration of longleaf pine, and provisioning of woodpecker clusters with artificial cavities and drilled starts, have been vital in improving habitat quality for red-cockaded woodpeckers on military lands (USFWS 2003). Such land management practices do not preclude the possibility that a small portion of woodpecker groups may be impacted by maneuver training operations and noise on military installations. We suggest that red-cockaded woodpecker adaptation to natural disturbance (i.e., fire and various depredation pressures) through cooperative breeding and re-nesting provide these birds with the necessary tools to deal with other disturbance factors (USFWS 2003). We also suggest that habitat quality (i.e., foraging habitat and adequate number of nesting and roosting cavities) plays an important role in a woodpecker's ability to cope with extraneous disturbance factors during the breeding season. Intensive habitat and population management in the form of mechanical midstory removal, artificial cavity provisioning, and translocation appear to dampen effects of suboptimal habitat quality (Spadgenske 2002, Spadgenske et al. 2005) and also may be appropriate mitigation for occasional reproductive losses due to military training operations.

Natural resource management policies on military installations have had a positive influence on recovery of red-cockaded woodpeckers (Doresky et al. 2001, Costa 2005). Active woodpecker groups have steadily declined on much of the private land in Georgia due to limitations in cavity tree availability, habitat fragmentation, poor foraging habitat, and ineffective burning regimes (Baker 1995). In contrast, woodpecker populations on Fort Stewart have increased steadily, largely in response to beneficial habitat management practices such as those described above. Since our field study concluded, potential breeding groups and active clusters have continued to steadily increase (Fig. 5; Carlile et al. 2005). This increase was not due to discovery of new woodpecker groups, but from creation of recruitment clusters in unoccupied habitat and during budding, when young from previous nests initiated nests themselves within the same cluster.

MANAGEMENT IMPLICATIONS

This research differs from previous noise disturbance studies in a number of important ways. First, we interpreted noise levels based on woodpecker-weighting algorithms, which is more specific to the subject animal's hearing sensitivity than the generalized and less applicable A- or unweighted algorithms. We found little evidence, though, that W-weighting is a better predictor than A-weighting of woodpecker flush response based on our sample sizes and level of testing, but more testing is warranted.

Our data indicate that infrequent, short-duration (<2 hr) military training exercises at the levels and for the noise sources tested close to active woodpecker nest sites did not impact woodpecker reproduction on the Fort Stewart Military Installation. We make this assertion with a few caveats, namely, that 1) we did not test military training operations that lasted >2 hours within woodpecker clusters, 2) we did not specifically test how habitat quality may influence woodpecker response behavior, 3) results are applicable only to the level and type of noise and maneuver testing (i.e., noise level, stimulus type, number and frequency of noise events, and disturbance distance) we recorded, and 4) we were not able to test if red-cockaded woodpeckers became sensitized or habituated to military training operations due to the endangered status of this species. We were authorized to conduct initial testing into potential responses of woodpeckers to military training operations to test a specific change in management guidelines, but we were not given permission to be too aggressive and potentially cause nest abandonment due to our experimental testing. We do not believe that military maneuver training noise is a limiting factor in the recovery of red-cockaded woodpeckers on military installations based on our level of and type of testing. Numbers of active, nesting, and successful red-cockaded woodpecker nests on Fort Stewart increased each year during our study (ESMPT 2001).

We do not suggest that woodpeckers cannot be disturbed by the military activities, but at the levels and for the types of stimuli we tested, we did not observe a significant impact on woodpecker reproduction or productivity. It is possible that louder, longer, and more-frequent disturbances (e.g., military encampment near an active woodpecker nest) and increased human presence could more negatively influence woodpecker nesting behavior. However, we believe we presented nesting woodpeckers with very aggressive military training levels at or above what most individuals within the population would experience during the nesting season. It is unknown what effect increased military range utilization, the introduction of other novel noises to inexperienced birds, or new weapons systems would have on this species. More research is needed to study the potential habituation and sensitization of red-cockaded woodpeckers to anthropogenic sources and to help answer many of the questions on this topic (Whittaker and Knight 1998).

SUMMARY

- Military training events on Fort Stewart did not significantly affect red-cockaded woodpecker reproductive success and productivity given the range and intensity (i.e., noise level, stimulus distance, group size, duration, and frequency of noise event) and type (weapons noise, aircraft and helicopter overflights, vehicle traffic) of anthropogenic noise sources tested.
- Experimental sites did not differ from control sites in number of eggs, nestlings, or fledglings produced.
- We believe the lack of differences in reproductive success and productivity between experimental and control groups was partially attributable to the ability of red-cockaded woodpeckers to cope with adversity through their dynamic breeding system. The ability of red-cockaded woodpeckers to excavate their own cavities, re-nest after brood loss, and possibly increase nesting potential through their use of helpers provides this species with some potential buffer against future disturbances.
- Downy woodpeckers, as surrogates for red-cockaded woodpeckers, had their best hearing sensitivity within the peak range of the power spectrum of both downy and red-cockaded woodpecker vocalizations, which is at a higher frequency than that of a typical passerine.
- Woodpeckers had reduced auditory sensitivity relative to other species of small birds, especially in the higher frequency (>4.0 kHz) range.
- Woodpeckers were most sensitive in the 1.5- to 4.0-kHz range. Sensitivity appeared to drop off quickly at frequencies below 1.0 kHz and above 4.0 kHz. More research is needed to further test hearing sensitivity of red-cockaded woodpeckers, especially at frequencies below 0.5 kHz.
- Red-cockaded woodpeckers flushed infrequently in response to military training noise during the 1998 through 2000 nesting seasons.
- Woodpeckers did not flush from nests when artillery simulator blasts and 0.50-caliber blank fire were >152.4 m away and SEL noise levels were <65 dBW (72 dB, unweighted) and <68 dBW (80 dB, unweighted), respectively.
- As stimulus distance decreased, flush frequency increased, regardless of stimulus type or year.
- Woodpeckers returned to nests within an average of 4.4 minutes and a maximum of 16.2 minutes after being flushed by artillery simulators. Return times were higher for 0.50-caliber blank-fire tests, averaging 6.3 minutes, with a maximum of 26.8 minutes.
- We observed fewer woodpecker arrivals to the nest during incubation and nesting after stimulus events than before disturbance events. The amount of reduction depended on the type of blast stimulus and number of helpers at the nest. Blast treatments had no detectable effects on nest attendance.
- Adult caretakers responded to disturbance by spending longer average bouts (i.e., more time) on the nest, at the cost of reducing the feeding rate after the blast, which could lead to reduced nest-attendance rates if stimulus events occur over extended periods or over multiple days during the incubation period. Helpers at nests during incubation appeared to offset any potential reduction in arrival rates by adults during disturbance events.
- Life-table analyses of flush response time showed that at short ranges (15–30 m) the flush response was stronger for artillery simulator blasts than for blank fire in both the incubation and the nestling phase. In contrast, at medium distances (45–60 m) blank fire tended to produce more flush responses than artillery fire in both incubation and nestling phases. At longer distances (>60 m) blank fire and artillery produced similar flush responses in the incubation phase, whereas flush response was stronger for blank fire than for artillery in the nestling phase.
- There is little evidence that W-weighting is a better predictor than A-weighting of woodpecker flush response based on our sample sizes and level of testing, but more testing is warranted.

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