J. Field Ornithol., 71(1):140-146

SPOTTED OWL TURNOVER AND REPRODUCTION IN MANAGED FORESTS OF NORTH-COASTAL CALIFORNIA

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Abstract.-Northern Spotted Owl (*Strix occidentalis caurina*) reproduction and turnover (when an owl died or shifted territories, and was replaced by another owl) were monitored at 51 locations on Simpson Timber Company lands, northwestern California, from 1991-1995. We tested for differences in proportions of five stand age classes and reproductive success between Spotted Owl pair sites with (≥1 turnover) and without turnovers. Owl pairs at sites without turnovers fledged more young, showed more consistent reproductive success, and were surrounded by a greater percentage of 21-40-yr-old stands than were owl pairs at sites with turnovers. We hypothesize that pairs with high mate fidelity and survival were more reproductively successful because those pairs had previous breeding experience together. By investigating turnover along with habitat features, we now have an indication of the relative quality of various habitats for Spotted Owls on managed, coastal forests of northern California.

REEMPLAZO Y REPRODUCCIÓN DE INDIVIDUOS DE *STRIX OCCIDENTALIS CAURINA* EN BOSQUES MANEJADOS DE LA COSTA NORTE DE CALIFORNIA

Sinopsis.-Se monitoreó la reproducción y reemplazo (cuando un ave moría o cambió su territorio y fué reemplazado por otra individuo) de individuos de *Strix occidentalis caurina* en 51 localidades en los terrenos de la Simpson Timber Company, en el norte de California entre 1991 y 1995. Examinamos las diferencias en las proporciones de cinco etapas serales de diferentes edades con el éxito reproductivo entre pares de aves con uno o más reemplazos y parejas sin reemplazo. Las parejas en lugares sin reemplazo criaron más pichones, mostraron un éxito reproductivo más constante y se rodearon por un mayor porcentaje de troncos viejos (de 21-40 años) que en parejas en lugares sin reemplazo. Hipotetizamos que las parejas con mayor fidelidad mutua y supervivencia fueron más exitosos reproductivamente porque esas parejas tenían experiencias previas de anidaje juntos. Al investigar la incidencia de reemplazo junto con las características del hábitat, tenemos al presente una indicación de la calidad relativa de varios habitats para esta especie en bosques manejados en las costas del norte de California.

In many avian species, breeding experience is associated with larger

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clutch sizes (Coulson 1970, Parmelee and Pietz 1987, Bradley et al. 1990, Wooler et al. 1990), egg sizes (Richdale and Warham 1973, Ollasen and Dunnett 1983, Weimerskirch 1990, Croxall et al. 1992), and earlier laying date (Coulson 1970, Brooke 1978, Ens et al. 1993). Moreover, in numerous bird species, the number of fledglings produced from established pairs and experienced females is higher than from newly formed pairs and inexperienced females (Coulson 1966, Kepler 1969, Wood 1971, Mills 1973, Davis 1976, Brooke 1978, Ollason and Dunnet 1978, Bryant 1979).

Despite the many investigations of this topic, there has been no research involving the effects of breeding experience and duration of pair bonds on reproductive success of the federally threatened Northern Spotted Owl (*Strix occidentalis caurina*). Lands in northwestern California, owned by Simpson Timber Company (STC), provide an opportunity to examine this question, as there resides a population of Spotted Owls that have been studied for many years. Spotted Owls are generally monogamous, and usually maintain the same home ranges from year to year (Forsman et al. 1984). Verner et al. (1991) observed that solitary migrating mates returned to their former summer home ranges and re-united with their previous mate, if both mates were still alive. Pair separations have been observed on STC lands, where owls re-paired with a new mate, but are a small percentage of re-pairing events. Because long-term pair bonds characterize the Spotted Owl's mating system, reproductive success resulting from established pair bonds (experienced pairs) can be compared to that from newly formed pair bonds (inexperienced pairs).

The clutch size of Spotted Owls is usually limited to no more than two eggs (Johnsgard 1988), and although three and four egg clutches occur (Dunn 1901, Forsman et al. 1984), they are infrequent. There has never been a documented case of a clutch larger than two eggs on STC lands. The low variability of Spotted Owl clutches limits investigations of experience on clutch size, and the Spotted Owl's threatened status precludes the handling of eggs to investigate egg size variation. Laying date is a difficult parameter to establish, as precarious nest locations and positions often constrain one's ability to detect the presence of eggs and/or nestlings within a nest. Consequently, we quantified the effect of pair experience on fledgling production. In addition, we examined associations of stand age with the occurrence of newly formed pair bonds. Our objectives were to evaluate differences in fecundity between sites with and without stable owl pairs and assess possible associations between Spotted Owl turnovers and forest stand age.

STUDY AREA AND METHODS

The study area is located in the North Coast, North Coast Range, and Klamath Range subregions of California (Hickman 1993) in Humboldt and Del Norte counties. These lands are primarily within 32 km from the coast, but extend up to 85 km inland in places. The subregions are characterized by redwood (*Sequoia sempervirens*), mixed-evergreen, and mixed-hardwood forests and by high rainfall. Climate, vegetation characteristics, and geographic location of the 120,000-ha study area are detailed in Thome et al. (1999). Because of clearcutting, STC's forests consist mainly of young (second and third growth) trees. Less than 1 % of the area is classified as old growth (>200 yr old), and the oldest forest stands in the remaining area are 80-90 yr old. Scattered residual trees (trees left uncut during past logging operations) occur in some stands. These residual trees are remnant from stands of both young seral stage and old-growth forests, and are older and larger than the dominant element of the stand.

We used the occurrence of Spotted Owl turnover events (i.e., when an owl pair member was replaced by another owl) as a measure of pair inexperience. Although it is possible that not all turnovers resulted in newly formed pair bonds, the majority of replaced birds (82%) were never found again. In addition, 50% of the new recruits were subadults (≤2 yr old). Because Spotted Owls generally do not breed until they are ≥2 yr old (Miller et al. 1985), the year that subadults were found as replacements would likely be their first year breeding. Thus, we used turnovers as indicators of pairs that had little or no experience breeding with each other.

We recorded Spotted Owl turnovers at >200 owl territories (sites) from March through August of 1991-1995, during a demography study on the Simpson Timberlands study area in northwestern California (Simpson Timber Company 1991) . From these territories, we selected those occupied by a pair for at least one of five years. In addition, we used only those sites containing ≥75% of their area within STC property when a 398-ha-circle (1.1-km radius) was drawn around the site center. This was to ensure sufficient Geographic Information System (GIS) coverage of habitat at those sites for analysis purposes. Fifty-one sites met these criteria.

A turnover was defined as an occasion when a known (banded) owl at a site, of either sex, was replaced by a different owl. For analysis, turnover at each site was tabulated as a binomial variable: 0 turnovers or ≥1 turnover during the study. We examined associations of turnovers with reproduction and stand age. Spotted Owl reproduction was monitored for the duration of this study (Thome et al. 1999).

Reproductive success was measured as the percentage of years that ≥1 young were successfully fledged and the mean number of fledglings per year. Both parameters were calculated based on the number of years that fledgling data were acquired. We had five years of data for 29 sites, four years for 17 sites, and three years for 5 sites. We used a 2 X 3 contingency table analysis to test for a possible bias detecting turnovers with sites having three, four, and five years of data. Stand ages were calculated using ARC/INFO version 7.0.4 at a 1.1-km radius surrounding pair sites (398 ha). This scale was chosen because California regulations mandate Spotted Owl surveys to be conducted within 1.1 km (0.7 mi.) of a proposed timber harvest plan (California Department of Forestry and Fire Protection 1997:81). Landscape data from 1995 were the only data available for

TABLE 1. Description of five stand age classes used in analysis of habitat surrounding Spotted Owl locations on Simpson Timber Company property in northern California, 1991-1995. Data were taken from a 398-ha circle surrounding site centers.

Stand age (yr)	Trees/ha $\bar{x} \pm$ SE	Basal area[a] $\bar{x} \pm$ SE	Volume[b] $\bar{x} \pm$ SE
0-5	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
6-20	5.82 ± 1.03	0.11 ± 0.03	0.01 ± 0.00
21-40	168.89 ± 6.03	10.99 ± 0.44	3.11 ± 0.14
41-60	214.30 ± 8.92	25.73 ± 1.06	10.69 ± 0.46
>60	201.58 ± 10.41	24.29 ± 1.13	14.87 ± 0.71

[a] Measured in m^2/ha.
[b] Measured in million board meters/ha.

use, and were considered adequate because less than 2% of the total area within the 398-ha owl circles contained clearcuts that were not present the year site locations were chosen.

To avoid pseudoreplication, stand ages were analyzed with respect to a single location for each owl site, taken from 5 years of data. Owl site locations were chosen based on guidelines in Thome et al. (1999). Forty-four Spotted Owl nest locations and seven pair locations were used in the analysis. Stand ages were calculated from the previous clearcut harvest date, and were placed into five categories: 0-5, 6-20, 21-40, 41-60, and >60 yr. The proportion of a given circle that was comprised of each age class was then calculated. The 60 yr cutoff was established because STC's average current rotation age (the age at which stands are harvested) is approximately 60 yr (B. Houston, STC Forester, pers. comm.). Stands >80 yr were pooled into the >60 yr category, because they were a mean of only 6.29% (SE = 1.82) of habitat within owl sites using a 398-ha circle. Size and density of trees in the five age classes are given in Table 1.

We hypothesized that owl sites with turnovers would have fewer fledglings, and would be successful less often than would sites without turnovers. If this was true, if followed that higher proportions of forest stands 21-40 yr old would be associated with the lack of turnovers, because higher proportions of 21-40-yr-old stands were associated with higher reproduction on STC lands (Thome et al. 1999). The effect of turnover on reproduction was assessed using two-tailed *t*-tests, and mean proportion of the five stand age classes were tested against the presence/absence of turnovers using Mann-Whitney *U*-tests because of lack of normality. Analyses were conducted using NCSS (Hintze 1995) . For all statistical analysis, significance was considered $P \leq 0.05$.

RESULTS

During the five years of study, 32 sites were occupied by a pair for 5 yr, 12 for 4 yr, and 7 for 3 yr. Turnovers occurred at 30 sites, 24 of which had one turnover, and six had two turnovers. Mean number of fledglings per year ranged from 0.0 to 1.6, with an overall average of 0.497 (SE =

TABLE 2. Results of stand age class composition comparisons (at a 398-ha scale) between Spotted Owl sites with (n = 30) and without (n = 21) turnovers on Simpson Timber Company property, northern California, 1991-1995.

	% owl site age class composition ($\bar{x} \pm$ SE)			
Stand age (yr)	With turnovers	Without turnovers	Z	P[a]
0-5	8.32 ± 1.37	10.91 ± 2.94	0.211	0.833
6-20	17.06 ± 3.70	18.03 ± 3.76	0.684	0.494
21-40	23.31 ± 4.52	36.04 ± 5.69	2.030	0.021
41-60	27.19 ± 4.72	17.58 ± 5.14	-1.008	0.313
>60	16.61 ± 3.42	12.17 ± 2.93	-0.654	0.513

[a] P-values are from Mann-Whitney U-tests comparing sites with and without turnovers.

.050; n = 51) . Mean proportion of years when young were successfully fledged ranged from 0.0 to 0.8, with an overall average of 0.338 (SE = 0.029; n = 51) . Our analysis showed that proportion of turnovers had no association with sites having three (80% had turnovers), four (47% had turnovers), or five (62% had turnovers) years of data (X^2 = 2.023, df = 2, P = 0.364) . Sites without turnovers produced more fledglings ($\bar{x}$ = 0.613, SE = 0.092) than did sites with turnovers ($\bar{x}$ = 0.416, SE = 0.053) (t = 1.983, df = 49, P = 0.053) . In addition, sites without turnovers showed a higher proportion of years when ≥1 owlet fledged ($\bar{x}$ = 0.403, SE = 0.046) than did sites with turnovers ($\bar{x}$ = 0.292, SE = 0.035) (t = 1.939, 49 df, P = 0.058) . Sites without turnovers had more forest of the 21-40 yr age class than sites with turnovers (Table 2). No significant differences were detected with other age classes.

DISCUSSION

Consistent with studies of other bird species, reproductive success was lower at sites with turnovers, which may reflect inexperience of pairs at nesting, foraging, and/or parenting in general. Because reproductive success is strongly associated with long-term pair bonds in many avian species (Rowley 1983, Mock and Fujioka 1990), the inexperience of the pair interacting together likely influenced reproduction. Under the constraint hypothesis (Curio 1983, Fowler 1995), young birds reproduce less well because they have not yet acquired the skills necessary for successful breeding. This also may have been a contributing factor in this study, as half of the new recruits were inexperienced subadults.

We found that owls occupying sites where turnovers occurred had poorer reproduction than did owls occupying sites without turnovers. This may be important for Spotted Owls that do not occupy high-quality habitat (i.e., habitat conferring high reproductive success), but have high mate fidelity or high survival. Because clearcuts on STC lands have been associated with lower reproductive success at 398 ha in a previous study (Thome et al. 1999), we expected clearcuts to be associated with turnovers as well. However, stands 0-5 yr old (recent clearcuts) were not associated with turnovers. Although clearcuts influence reproductive success, they apparently do not contribute to factors causing turnover in this study area.

We anticipated higher percentages of stands 21-40 yr old to be associated with sites lacking turnovers because this age class was also associated with higher reproduction. We hypothesize that the stability of pairs at sites with higher proportions of 21-40 yr-old stands may be a result of higher woodrat (*Neotoma fuscipes*) abundance and/or availability in those stands (Thome et al. 1999), but this explanation has yet to be tested. Regardless of the explanation, stands surrounding sites without turnovers had 12.73% more forest in the 21-40 yr age class than did sites with turnovers (Table 2). This result warrants further investigation into the qualities of young stands (21-40 yr) that facilitate the stability of Spotted Owl pairs.

ACKNOWLEDGMENTS

We thank J. M. Beck, G. H. Brooks, D. E. Copeland, L. B. Folliard, K. A. Hamm, C. A. Hibbard, R. R. Klug, B. D. Michaels, J. L. Thompson, and B. J. Yost for their exceptional field work. D. Opalach, G. N. Warinner, and J. E. Bishop were very patient in helping with Simpson's GIS data. Earlier drafts of this manuscript were improved by comments from T. W. Arnold, J. A. Blakesley, J. B. Buchanan, M. A. Colwell, J. R. Dunk, C. Ogan, J. R. Waters, and an anonymous reviewer. Simpson Timber Company funded this research.

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Received 23 Nov. 1998; accepted 24 May 1999.