



## LIFE-HISTORY TRADEOFFS IN SPOTTED OWLS (*STRIX OCCIDENTALIS*): IMPLICATIONS FOR ASSESSMENT OF TERRITORY QUALITY

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**ABSTRACT.**—Tradeoffs among life-history traits have long provided material for evolutionary studies of life-history strategies but can also have practical implications for assessments of habitat and territory quality in species of conservation concern. Here, we characterize tradeoffs between parental reproductive output and offspring fitness in a closed population of California Spotted Owls (*Strix occidentalis occidentalis*) using multistratum mark–recapture models and evaluate how potential tradeoffs influenced measures of territory quality. We detected heterogeneity in offspring survival associated with parental reproductive output; individuals that fledged in pairs had a greater probability of surviving than individuals that fledged either as singletons or in triplets, an advantage that was evident in juvenile, subadult, and adult life stages. Thus, the survivorship of offspring that fledged in pairs was high despite costs associated with producing a second fledgling, but the demands of producing a third fledgling came at a cost to offspring survival. Age of recruitment into the territorial population and the future reproductive output of offspring were not related to parental reproductive output in the year of birth. Indices of territory quality based on parental reproductive output were correlated with indices of territory quality based on offspring fitness despite the heterogeneity in offspring fitness associated with parental reproductive output. Our results suggest that ranking territories for conservation planning on the basis of parental reproductive output can be useful in territorial species, but the generality of this finding should be evaluated across a range of life histories. Received 8 May 2012, accepted 26 September 2012.

**Key words:** fitness, life-history tradeoffs, recruitment, reproductive output, Spotted Owl, survival probability, territory quality.

### Compromisos en la Historia de Vida de *Strix occidentalis*: Implicaciones para la Evaluación de la Calidad de los Territorios

**RESUMEN.**—Los compromisos entre algunos rasgos de la historia de vida han sido materia de estudio en trabajos sobre la evolución de las estrategias de historia de vida, pero también pueden tener implicaciones prácticas para la evaluación de la calidad de los hábitats y de los territorios en especies de importancia para la conservación. Caracterizamos los compromisos entre el rendimiento reproductivo de los padres y la aptitud de las crías en una población cerrada de *Strix occidentalis occidentalis* usando modelos de marcado-recaptura con múltiples estratos, y evaluamos cómo los compromisos potenciales influyen en las medidas de la calidad de los territorios. Detectamos heterogeneidad en la supervivencia de las crías asociada con el rendimiento reproductivo de los padres. Los individuos que emplumaron en parejas tuvieron una mayor probabilidad de sobrevivir que los que emplumaron como hijos únicos o en tripletas, ventaja que fue evidente en la etapa juvenil, sub adulta y adulta. Así, la supervivencia de las crías que emplumaron en parejas fue alta sin importar los costos asociados con la producción de un segundo polluelo, pero las demandas de producir un tercer polluelo representaron un costo en términos de la supervivencia de la descendencia. La edad de reclutamiento en la población territorial y el rendimiento reproductivo futuro de las crías no estuvieron relacionados con el rendimiento reproductivo parental en el año de nacimiento. Los índices de la calidad de los territorios basados en el rendimiento reproductivo de los padres se correlacionaron con aquellos basados en la aptitud de las crías, sin importar la heterogeneidad de la aptitud de las crías asociada con el rendimiento reproductivo de los padres. Nuestros resultados sugieren que la categorización de los territorios para los planes de conservación con base en el rendimiento reproductivo parental puede ser útil en especies territoriales, pero la generalidad de este resultado aún debe ser evaluada a través de un espectro de diferentes historias de vida.

**THEORY PREDICTS THAT** individual fitness is constrained by tradeoffs among life-history traits and that, as a result, natural selection should favor individuals that allocate resources in a manner that balances tradeoffs and maximizes lifetime reproductive output (Roff 1992,

Stearns 1992). Since David Lack hypothesized that females lay clutches of a size that maximizes the product of clutch size and offspring survival (Lack 1947), the potential tradeoff between parental reproductive output and offspring fitness has been a topic of intense interest in

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evolutionary ecology (e.g., Pettifor et al. 1988, 2001; Murphy 2000; de Heij et al. 2006). Indeed, costs of reproduction for offspring fitness, whereby increased parental reproductive output comes at a cost to offspring survivorship, have been detected in many animal species (Lindén and Møller 1989, Jacobsen et al. 1995, Murphy 2000, de Heij et al. 2006). However, life-history tradeoffs can be obscured by various factors (Lindén and Møller 1989, Reid et al. 2003, Risch et al. 2007), one being variation in individual quality, whereby high-quality individuals are more likely to produce large numbers of young with high survival probabilities (Hamel et al. 2009). Thus, traits may covary positively in higher-quality individuals but exhibit negative covariation in low-quality individuals, as expected under classic models of life-history tradeoffs.

Although covariation in traits has been central to evolutionary studies of life-history strategies, the recognition that life-history tradeoffs can influence population processes is more recent (Silvertown and Dodd 1999, Proaktor et al. 2008). Indeed, the link between life-history tradeoffs and population processes suggests that covariation in traits may have important implications in demographic assessments of species of conservation concern (Low and Pärt 2009). For example, negative or positive covariation between breeding effort and juvenile survival can influence assessments of habitat quality in territorial species, which is commonly inferred by relating the number of young produced to territory-specific habitat conditions without considering offspring survival (Franklin et al. 2000, Johnson 2007, Gołowski and Meissner 2008). If, for example, more young are produced in certain territories, habitat features present in those territories (or the territories themselves) are considered important to population-level reproductive output and are targeted for management (U.S. Fish and Wildlife Service [USFWS] 2007, Vander Haegen 2007). However, the value of high-quality territories and habitats will be underestimated if there is positive covariation between parental reproductive output and offspring fitness. Conversely, negative covariation between parental reproductive output and offspring fitness would homogenize differences in the relative contributions of different territories and habitats to population growth.

Here, we characterize possible tradeoffs between reproductive output (defined as the number of young produced in a given breeding event) and offspring fitness in a population of California Spotted Owls (*Strix occidentalis occidentalis*; hereafter, Spotted Owls) and evaluated how tradeoffs influenced assessments of territory quality. The Spotted Owl is a good species for testing predictions about life-history tradeoffs because (1) it employs a “bet-hedging” reproductive strategy and produces a variable number of offspring per breeding attempt (Franklin et al. 2000, Seamans and Gutiérrez 2007); (2) long-term demographic studies estimating Spotted Owl vital rates have been conducted using rigorous, standardized methods (Franklin et al. 1996, Blakesley et al. 2010); and (3) our particular study population is essentially closed to emigration, such that juveniles have a high probability of remaining in the study area once they enter the territorial population and are very likely to be detected if they become territorial (LaHaye et al. 2001, Zimmerman et al. 2007). Specifically, we tested the hypothesis that offspring produced in large broods are less likely to survive to adulthood, have delayed recruitment into the territorial population, and experience lower reproductive success than offspring produced in small broods. We then determined whether indices of territory quality based on parental

reproductive output are biased by ignoring tradeoffs between reproductive output and offspring fitness.

## METHODS

*Study area and field work.*—We conducted our study from 1987 to 1998 in the San Bernardino Mountains (34°10′N, 117°00′W), about 140 km east of Los Angeles, California. In 1987, we established the 535-km<sup>2</sup> study area centered on the majority of the Spotted Owl locations known at that time. In 1989, we expanded the study area to include the entire 2,137-km<sup>2</sup> San Bernardino Mountains. Each year, we systematically surveyed all previously occupied Spotted Owl locations as well as all other forested vegetation in the range. We conducted nighttime surveys to locate individuals by imitating Spotted Owl vocalizations for ≥15 min at each call point (spaced ~0.8 km apart) or by calling continuously while walking designated survey routes (Forsman 1983, Franklin et al. 1996). We returned to the area of each response at dawn and attempted to relocate owls visually (i.e., “walk-in” survey). During walk-in surveys, we fed live mice to adult owls to assess reproductive status and locate nests (Forsman 1983, Franklin et al. 1996). A pair was classified as not having nested in a given year if the female roosted for >45 min continuously without tending young on at least one visit prior to 15 May (Blakesley et al. 2010). If either member of a nesting pair took ≥4 mice without delivering ≥1 mouse to young, the nest was considered to have failed. The number of young fledged from successful nests was determined by feeding parents mice, their subsequent delivery of prey to young, and visual searches of the nest stand. Fledgling numbers likely constitute a reasonable estimate of reproductive output because parents typically alternate the young to which they deliver offered mice, juvenile owls typically occur together or in very close proximity to one another, and we visited nesting territories as soon as possible following the expected fledging date to minimize the effects of juvenile mortality. We attempted to capture and band all Spotted Owls using a noose pole or mist net. We banded adult and subadult owls with both USFWS and uniquely colored leg bands. Juveniles were fitted with a color band unique to each cohort and then recaptured and fitted with a unique color band when they entered the territorial population. We identified previously color-banded owls using binoculars and determined the sex of nonjuvenile owls by voice, behavior, or morphological measurements (Forsman 1983, Franklin et al. 1996). The sex of juveniles was not determined until owls originally banded as juveniles were recaptured.

*Effect of parental reproductive output on offspring survival and age of recruitment.*—We tested for possible effects of parental reproductive output on offspring survival and age of recruitment into the territorial population using multistatum mark–recapture models implemented in Program MARK (White and Burnham 1999), based on encounter histories of owls originally captured as juveniles. Multistatum models provided a convenient framework for jointly modeling the effect of parental reproductive output on apparent survival rates ( $\phi$ ), recapture rates ( $p$ ), and transition probabilities among states ( $\psi$ ; White et al. 2006). We treated territorial and nonterritorial owls as the only two states in the model where nonterritorial owls of age  $i$  could transition (i.e., recruit) into the territorial state according to the transition probability  $\psi_i$  conditional on survival

(Pradel and Lebreton 1999). Using multistratum models to estimate  $\psi_j$  allowed us to account for the fact that not all territory holders were recaptured in the year they recruited into the territorial population. We considered the nonterritorial state to be “unobservable” because nonterritorial owls rarely respond to imitated vocalizations and are rarely identified. According to the multistratum model, recapture probabilities represented both the probability of physically recapturing individuals marked with cohort bands when they became territory holders and the probability of resighting individuals with unique color bands. The model assumed that survival did not differ between nonterritorial and territorial states and that recapture probabilities did not differ between the initial year of recruitment and subsequent years (Pradel and Lebreton 1999). The first assumption was not testable, but we doubted that lower recapture probabilities in the initial year of recruitment (due to the need to physically capture individuals with cohort-bands) biased our estimates, because only 3 of 130 territory holders were not captured in the first year they were observed. Although we believed that our study population was demographically closed and that we surveyed virtually all owl habitat in the range, some individuals may have gone undetected, such that our estimates reflected “apparent” rather than true survival. Nevertheless, for convenience we have used the term “survival” when discussing apparent survival because we believe that any such biases are slight.

We considered four stage classes for survival estimation in the multistratum model: juveniles (zero years of age at sampling), 1-year-old subadults, 2-year-old subadults, and adults ( $\geq 3$  years old). We treated parental reproductive output in the year of the offspring's birth as a categorical explanatory variable for offspring survival and classified reproductive output as either 1, 2, or  $\geq 3$  young fledged (4 young were observed to have fledged in only one instance). Subadult and adult survival were modeled as constant over time because little temporal variability existed in this parameter (LaHaye et al. 2004), but we allowed juvenile survival to vary among years.

We modeled the probability of transitioning from the nonterritorial to the territorial state as a function of age and parental reproductive output. We considered age, rather than stage, because 9% of individuals had not recruited by their third year (i.e., when they reached adulthood). For age, we considered both a linear trend where the probability of obtaining a territory was expected to increase with age ( $\psi_A$ ) and an age-specific structure where transition probabilities varied independently among ages ( $\psi_A$ ). Almost all juveniles (98%) had recruited into the territorial population by the time they were 4 years old; therefore, we constrained annual transition probabilities for nonterritorial owls in their 5th through 11th years to 1.0 for all models. We assumed that territorial owls remained territory holders until their death and fixed the transition probability from the territorial to nonterritorial state at zero.

We fixed recapture probabilities for nonterritorial owls at zero to reflect the fact that they are rarely detected and constituted an unobservable state. Recapture probabilities for territorial owls were modeled as a function of stage class ( $p_{\text{stage}}$ ), parental reproductive output ( $p_{\text{RO}}$ ), year ( $p_t$ ), and mean reproductive output (mean number of young produced per territorial pair) in year  $t$  ( $p_{\text{mRO}}$ ). We considered mean reproductive output as an annual covariate affecting recapture probabilities because previous

analyses indicated that our capture data fit this structure well and because it required only one additional parameter, as opposed to 10 for year effects (LaHaye et al. 2004, Peery et al. 2012).

We treated model  $\phi_{\text{stage} \times \text{RO} + t}$ ,  $P_{\text{stage} \times \text{RO} + t}$ ,  $\Psi_{\text{age} \times \text{RO}}$  as the global model. We did not consider time effects on transition probabilities, the effect of interactions between age and parental reproductive output on transition probabilities, or interactions involving temporal effects, because doing so resulted in a large number of inestimable parameters. Otherwise, we considered all possible combinations of main effects and two-way interactions. To limit the number of models, we sequentially determined the “best” model structure for recapture probabilities, transition probabilities, and survival probabilities. We used quasi-Akaike's information criterion corrected for small sample size (QAIC<sub>c</sub>) and QAIC<sub>c</sub> weights ( $w_j$ ) to rank competing models and account for overdispersion (Burnham and Anderson 2002; see below).

*Effect of parental reproductive output on offspring reproduction.*—We tested for the effect of parental reproductive output on subsequent reproduction by their offspring using a two-way analysis of variance. We treated offspring reproductive output in year  $t$  as the dependent variable. We treated offspring stage class (1-year-old subadult, 2-year-old subadult, or adult) in year  $t$ , parental reproductive output in the year of the offspring's birth, and the interaction between stage class and parental output as explanatory factors.

*Effect of life-history tradeoffs on assessments of territory quality.*—We used two approaches to assess the effect of ignoring life-history tradeoffs on assessments of territory quality. First, we related an index of territory quality based only on parental reproductive output to an index based on the observed number of offspring that recruited into the territorial population, while taking into account annual variation in these rates. Specifically, we calculated the index of territory quality based on parental reproductive output for territory  $i$  as follows:

$$Q_{\text{RO},i} = \frac{\sum_j (\text{RO}_{ij} - \overline{\text{RO}}_i)}{n_i}$$

where RO is the number of fledglings,  $j$  is the year for which reproductive data were available for territory  $i$ , and  $n$  is the number of years for which reproductive data were available (Blakesley et al. 2006). We calculated the index of territory quality based on the number of successful recruits as follows:

$$Q_{\text{RC},i} = \frac{\sum_j (\text{RC}_{ij} - \overline{\text{RC}}_i)}{n_i}$$

where  $\text{RC}_{ij}$  is the number of recruits that originally fledged from territory  $i$  in year  $j$ .

The second approach involved developing an index of territory quality based on the net reproductive value of juveniles that fledged as singletons, in pairs, and in triplets, and relating this index to  $Q_{\text{RO},i}$ . Net reproductive output represents the expected number of female offspring produced by a female over her lifetime (Caswell 2001) and, thus, constitutes a useful measure of the fitness of individual offspring. The index was calculated by multiplying the expected net reproductive value ( $\text{RV}_0$ ) of the offspring produced in each breeding event ( $\text{RC}_{ij}$ ) and then averaging the resultant sum across years for territory  $i$  as follows:

$$Q_{RV,i} = \frac{\sum_j \left( RO_{ij} RV_o - \frac{\sum_i RO_{ij} RV_o}{n_j} \right)}{n_i}$$

We estimated net reproductive value for each level of reproductive output (1, 2, or 3) separately using a postbreeding nine-stage class matrix model. The stages consisted of juveniles, 1-year-olds, 2-year-olds, 3-year-olds, and >3-year-olds, the latter four of which were further broken into both territorial and nonterritorial classes for a total of nine stages (Fig. 1). The model was parameterized with estimates of survival and transition probabilities derived from the highest-ranked multistratum model as well as fecundity estimates derived from the analysis of offspring reproductive output. Fecundity was estimated as half of reproductive output under the assumption of a 50:50 juvenile sex ratio. Net reproductive value was calculated from the left eigenvector of the matrix (Caswell 2001).

We used separate regression analyses to relate  $Q_{RC,i}$  and  $Q_{RV,i}$  to  $Q_{RO,i}$ , where  $Q_{RO,i}$  was treated as the dependent variable to determine how well fitness-based indices of territory quality could be predicted from parental reproductive output. For both analyses, we added a quadratic term for  $Q_{RO,i}$  to determine whether relationships were nonlinear, as might be expected if tradeoffs between parental reproductive output and offspring survival reduced fitness in territories with high or low reproductive output.

RESULTS

We assessed reproductive status at 127 Spotted Owl territories from 1987 to 1998. Estimating the exact proportion of all territories in the San Bernardino Mountains that were located was not possible, but we believe that we nearly censused the territorial population given the extensive surveying conducted throughout suitable owl habitat. We captured and banded 478 of the 508 juveniles (94%) located at these territories (juveniles captured in 1998 were not considered because the study ended in that year). We captured 143 juveniles (29.9%) that fledged as singletons, 234 (59.2%) that fledged in pairs, and 52 (10.9%) that fledged as triplets or quadruplets (only 4 juveniles were captured as part of a quadruplet). We recaptured 129 (27.0%) of these individuals as territory holders in subsequent years. The mean percentage of the known territorial population that was banded at the beginning of each year was 92% (LaHaye et al. 2001).

*Effect of parental reproductive output on offspring survival and age of recruitment.*—Bootstrap goodness-of-fit tests in Program MARK indicated that the global model did not fit the data ( $P < 0.01$ ). However, overdispersion was modest ( $\hat{c} = 1.38$ ); therefore, we used QAIC<sub>c</sub> to rank competing multistratum models.

The best model for recapture probabilities ( $\phi_{\text{stage}+RO}$ ,  $P_{RO}$ ,  $\psi_{\text{age}+RO}$ ) indicated that juveniles that fledged as singletons had a higher recapture probability ( $\pm$  SE;  $p = 0.965 \pm 0.040$ ) than juveniles that fledged in pairs or triplets ( $p = 0.795 \pm 0.038$  and  $p = 0.793 \pm 0.147$ , respectively). This model was ranked 0.8 QAIC<sub>c</sub>.

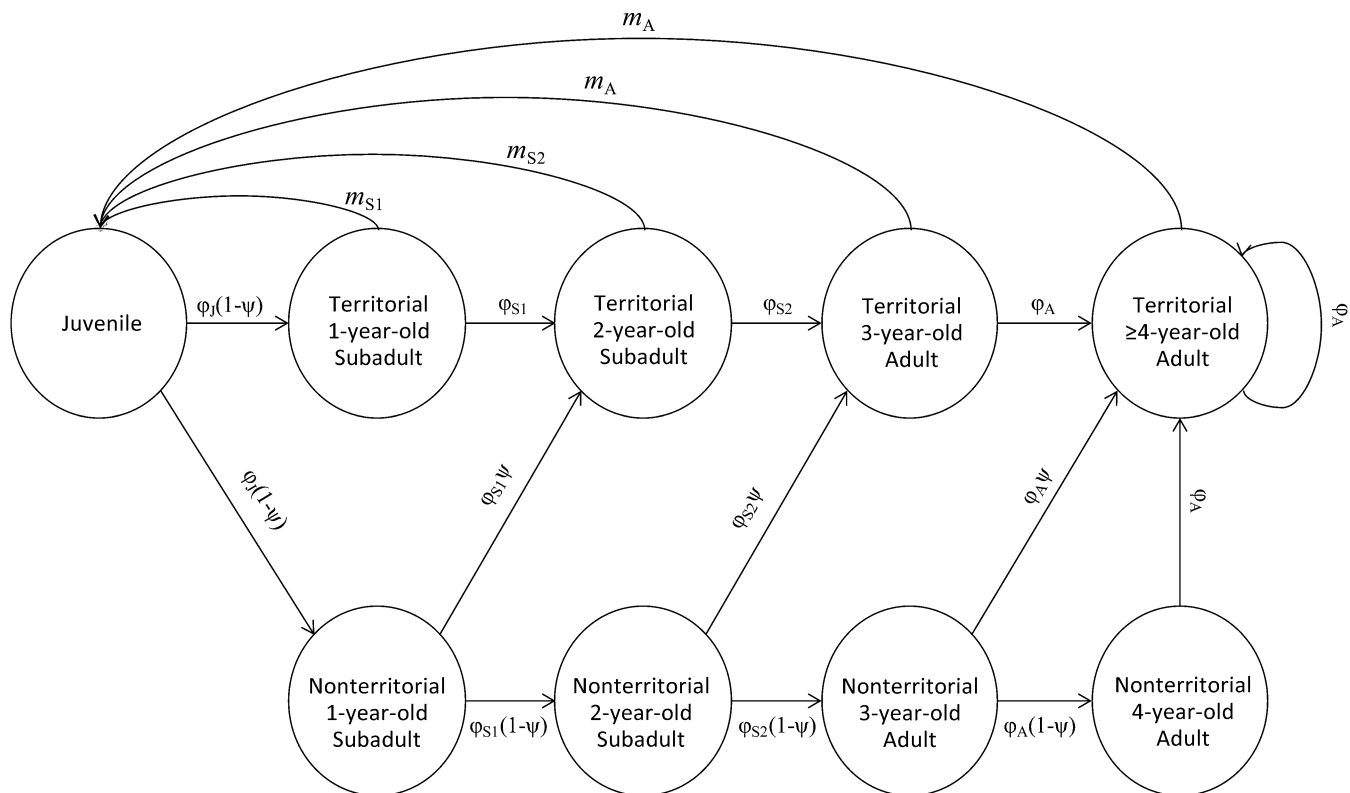


FIG. 1. Life-cycle diagram for a nine-stage class population model used to estimate net reproductive value in California Spotted Owls. The subscripts "A", "S2", "S1" and "J" refer to adults, 2-year old subadults, 1-year old subadults, and juveniles, respectively. The parameters  $m$ ,  $\psi$ , and  $\phi$  refer to fecundity, nonterritorial to territorial transition probabilities, and survival probabilities, respectively.

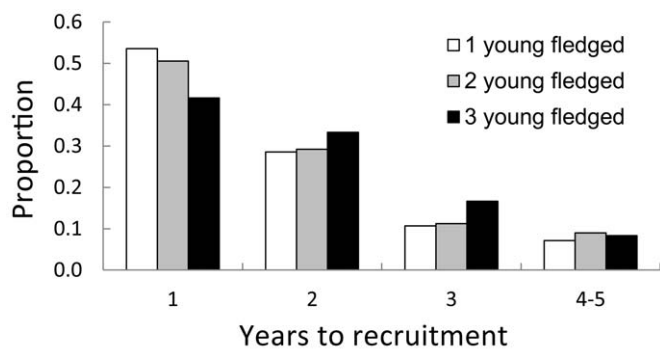


FIG. 2. Observed age of recruitment for California Spotted Owls in the San Bernardino Mountains from 1987 to 1998 as a function of parental reproductive output in the year of the offspring's birth.

higher and was 1.51× more likely (based on QAIC<sub>c</sub> weights) than the second-best model ( $\phi_{\text{stage}^*\text{RO}^*t}$ ,  $p$ ,  $\psi_{\text{age}^*\text{RO}}$ ) and was used for subsequent modeling of transition and survival probabilities.

The best model for transition probabilities ( $\phi_{\text{stage}^*\text{RO}^*t}$ ,  $p_{\text{RO}}$ ,  $\psi$ ) indicated that the probability of a nonterritorial individual recruiting into the territorial population was independent of parental reproductive output and offspring age until the offspring's fifth year (when  $\psi$  was fixed at 1.0). Indeed, the observed (naive) age of recruitment was very similar among Spotted Owls born as singletons, in pairs, or in triplets (Fig. 2). The only competing model for transition probability ( $\phi_{\text{stage}^*\text{RO}^*t}$ ,  $p_{\text{RO}}$ ,  $\psi_{\text{AGE}}$ ;  $\Delta\text{QAIC}_c = 1.2$ ) suggested that transition probabilities increased linearly from  $0.439 \pm 0.057$  in the first year to  $0.630 \pm 0.147$  in the fourth year. As a result, we used  $\psi$  to model variation in transition probabilities for all subsequent modeling of juvenile survival.

Model  $\phi_{\text{stage}^*\text{RO}}$ ,  $p_{\text{RO}}$ ,  $\psi$  was the highest-ranked survival model, which suggests that survival varied as a function of stage and parental reproductive output (Table 1). This model was 4.5× more supported than a model without parental reproductive output ( $\phi_{\text{stage}}$ ,  $p_{\text{RO}}$ ,  $\psi$ ; i.e., the second-best model), which indicates strong support for differences in offspring survival related to parental reproductive output. According to the top-ranked model, survival was greatest for individuals that fledged in pairs, and

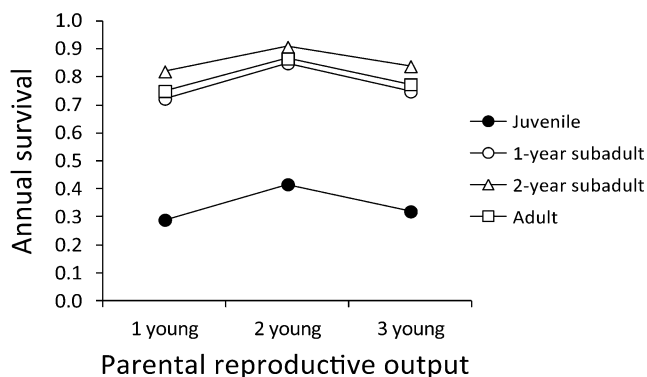


FIG. 3. Survival probabilities of California Spotted Owls in the San Bernardino Mountains as a function of parental reproductive output.

relatively low for individuals that fledged as singletons or in triplets (Fig. 3). Variation in survival associated with parental reproductive output was mirrored by the proportion of juveniles banded as singletons, in pairs, and in triplets that were later recaptured as territory holders (i.e., naive estimates of recruitment; 0.196, 0.314, and 0.231, respectively). Moreover, the top model was 54× more supported than a model containing an interaction between age and parental output ( $\phi_{\text{age}^*\text{RO}}$ ,  $p_{\text{RO}}$ ,  $\psi$ ; Table 1), which suggests that differences in survival due to parental reproductive output occurred in all stages considered (i.e., juvenile through adult; Fig. 3).

*Effect of parental reproductive output on offspring reproduction.*—We detected a strong effect of stage class on mean offspring reproductive output ( $F = 5.74$ ,  $df = 2$  and  $310$ ,  $P = 0.004$ ; 1-year-old subadult:  $0.304 \pm 0.093$ ; 2-year-old subadult:  $0.508 \pm 0.106$ ; adult:  $0.778 \pm 0.059$ ). However, neither parental reproductive output ( $F = 0.92$ ,  $df = 2$  and  $310$ ,  $P = 0.405$ ) nor the interaction between age and parental output ( $F = 0.77$ ,  $df = 4$  and  $310$ ,  $P = 0.548$ ) were significant predictors of offspring reproductive output.

*Effect of life-history tradeoffs on assessments of territory quality.*—The index of territory quality based on reproductive output ( $Q_{\text{RO},i}$ ) was a good predictor of the index of territory quality based on the number of recruits produced ( $Q_{\text{RC},i}$ ;  $F = 30.22$ ,  $df = 1$  and  $115$ ,  $P < 0.001$ ) using territories with at least three breeding

TABLE 1. QAIC<sub>c</sub> table for multistratum mark–recapture models analyzing Spotted Owl survival probabilities ( $\phi$ ), territory transition probabilities ( $\psi$ ; the probability of a nonterritorial owl recruiting into the territorial population), and recapture probabilities ( $p$ ). QAIC<sub>c</sub> = quasi-Akaike's information criterion corrected for small sample size,  $\Delta\text{QAIC}_c$  = the difference in QAIC<sub>c</sub> between model  $i$  and the highest-ranked model,  $k$  = number of parameters, and  $w_i$  = model weight. Model notation: the subscript "stage" refers to models with a stage-class effect (juvenile, 1-year-old subadult, 2-year-old subadult, and adult); the subscript "age" refers to models with an effect (0, 1, 2, 3, or  $\geq 4$  years old); the subscript "RO" refers to models with parental reproductive output as a factor; and the subscript "mRO" refers to models with population mean reproductive output as an annual covariate. Only models with  $w_i > 0.01$  are shown.

Survival models <sup>a</sup>				Transition models <sup>b</sup>				Recapture models <sup>c</sup>			
Model	$k$	$\Delta\text{QAIC}_c$	$w_i$	Model	$k$	$\Delta\text{QAIC}_c$	$w_i$	Model	$k$	$\Delta\text{QAIC}_c$	$w_i$
$\phi_{\text{stage}^*\text{RO}}$	10	0.0	0.806	$\psi$	25	0.0	0.546	$p_{\text{RO}}$	30	0.0	0.433
$\phi_{\text{stage}}$	8	3.0	0.179	$\psi_{\text{AGE}}$	26	1.2	0.304	$p$	28	0.8	0.287
$\phi_{\text{stage}^*\text{RO}}$	15	7.9	0.015	$\psi_{\text{RO}}$	27	4.2	0.067	$p_{\text{RO}^*\text{mRO}}$	31	2.1	0.150
				$\psi_{\text{age}}$	28	5.2	0.041	$p_{\text{RO}}$	29	3.0	0.099
				$\psi_{\text{AGE}^*\text{RO}}$	28	5.4	0.037	$p_{\text{stage}^*\text{RO}}$	33	5.9	0.022

<sup>a</sup>  $p_{\text{RO}}$  and  $\psi$  used for all survival models.

<sup>b</sup>  $\phi_{\text{stage}^*\text{RO}^*t}$  and  $p_{\text{RO}}$  used for all transition probability models.

<sup>c</sup>  $\phi_{\text{stage}^*\text{RO}^*t}$  and  $\psi_{\text{age}^*\text{RO}}$  used for all recapture models.

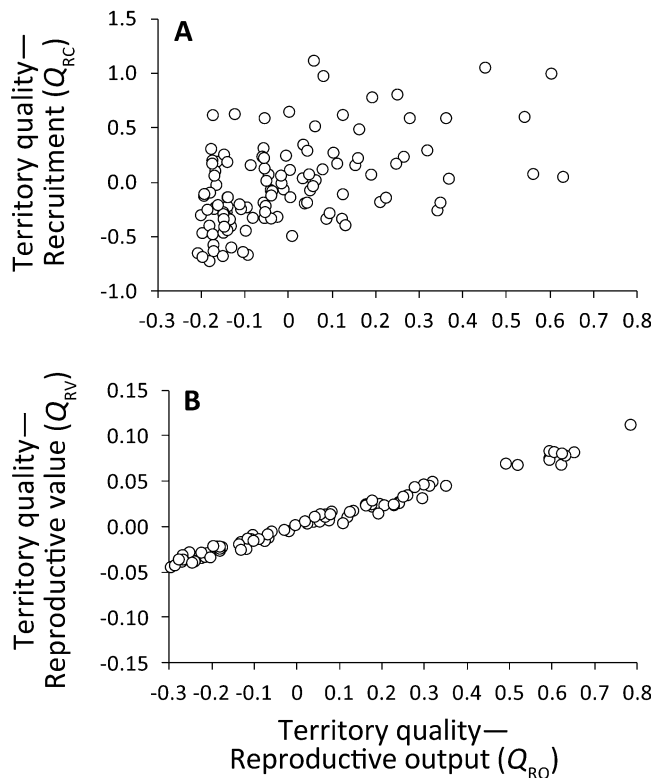


FIG. 4. Relationship between an index of California Spotted Owl territory quality in the San Bernardino Mountains based on parental reproductive output and (A) an index of territory quality based on offspring recruitment or (B) an index based on offspring net reproductive value.

attempts ( $n = 118$ ). The relationship between the two indices appeared to be linear, in that the quadratic term for  $Q_{RO,i}$  was not significant ( $F = 0.01$ ,  $df = 1$  and  $115$ ,  $P = 0.931$ ; Fig. 4A). However, by itself,  $(Q_{RO,i})$  explained a modest amount of the variation in  $Q_{RC,i}$  ( $R^2 = 0.23$ ).

We estimated that the net reproductive value of individual offspring was 0.115, 0.138, and 0.122 when parental reproductive output was 1, 2, and 3 young, respectively, using parameter values in Table 2. Indices of territory quality based on offspring net reproductive value ( $Q_{RV,i}$ ) and parental reproductive output ( $Q_{RO,i}$ ) were almost perfectly related ( $F = 12,408.7$ ,  $df = 1$  and  $115$ ,  $P < 0.001$ ,  $R^2 = 0.99$ ; Fig. 4B). The quadratic term for  $Q_{RO,i}$  was not significant ( $F = 2.4$ ,  $df = 1$  and  $115$ ,  $P = 0.128$ ), indicating that the relationship between the two indices was linear.

**DISCUSSION**

Spotted Owls that produced an intermediate number of young (i.e., 2 vs. 1 or 3) had a clear advantage in terms of the survivorship of their offspring. Indeed, juvenile survival was 1.44× greater for offspring that fledged in pairs than for offspring that fledged as singletons; similarly, subadult and adult survival was 1.11–1.18 times greater for offspring that fledged in pairs than for those that fledged as singletons. These results contrast with classic hypotheses about tradeoffs between reproductive effort and offspring survival, where the increased effort required to raise many young

TABLE 2. Values used to parameterize a matrix-based population model for California Spotted Owls and estimate net reproductive value as a function of parental reproductive output.

Parameter	Symbol	Parental reproductive output		
		1	2	3
<b>Survival probabilities</b>				
Juvenile	$\phi_J$	0.290	0.417	0.320
1-year-old subadult	$\phi_{S1}$	0.723	0.849	0.749
2-year-old subadult	$\phi_{S2}$	0.820	0.908	0.839
Adult	$\phi_A$	0.750	0.867	0.774
<b>Nonterritorial to territorial transition probabilities</b>				
All nonterritorial stage classes	$\psi$	0.474	0.474	0.474
<b>Fecundity</b>				
1-year-old subadult	$m_{S1}$	0.152	0.152	0.152
2-year-old subadult	$m_{S2}$	0.254	0.254	0.254
Adult	$m_A$	0.389	0.389	0.389

is predicted to compromise the fitness of offspring (Lack 1947). Rather, higher survival for offspring that fledged in pairs is consistent with the hypothesis that high-quality parents, or parents with access to higher-quality resources, are capable of producing many young with high survival probabilities (Hamel et al. 2009). Low survivorship in singletons could have occurred because poor environmental years in which most breeding pairs fledged only one young were also characterized by low juvenile survival. However, we found little support for annual variation in juvenile survival, and annual estimates of juvenile survival from the best model with a year effect were uncorrelated with annual estimates of mean reproductive output ( $P = 0.09$ ). Instead, we suspect that the ability of parents to raise more than one offspring varied idiosyncratically in space and time because of the interactive effects of habitat and annual weather conditions (Franklin et al. 2000), as well as parental quality and experience (Blakesley et al. 2006, Gutiérrez et al. 2011).

Although we observed positive covariation between parental reproductive output and offspring survival when two as opposed to one young were fledged, we observed a tradeoff between these two fitness components when parents fledged three as opposed to two young. Specifically, survival probabilities for juveniles that fledged in pairs were 1.30× greater than those for juveniles that fledged in triplets, and subadult and adult survival was 1.13–1.16 times greater for juveniles that fledged in pairs. Thus, our data suggested that breeding Spotted Owls incurred a cost, measured in the survivorship of their offspring, when they produced more than two young. This reduction in offspring survival is consistent with the classic hypothesis that the provisioning of young is constrained by an upper limit to the amount of food resources that a parent can procure. However, we cannot rule out the possibility of alternative explanations such as greater predation rates in triplets because parents spend a greater amount of time away from the nest foraging.

Greater survival in offspring that fledged in pairs was detected for all stage classes considered (juveniles, 1-year-old subadults, 2-year-old subadults, and adults), which suggests that the

advantages occurred beyond the first year of life. It is possible that nutritional stress incurred prior to independence affected development and had long-term fitness consequences. Indeed, experimental studies in birds have demonstrated that restricted diets during the nestling stage can result in reduced adult body size and mass (Searcy et al. 2004, Sears and Hatch 2008), lower social status (Richner et al. 1989), and, ultimately, reduced survival to adulthood (Tschirren et al. 2009). No effect of parental reproductive output was detected on the future reproduction of offspring; presumably, singletons and triplets that survived were in sufficiently good condition to reproduce at the same rate as offspring that fledged in pairs.

Parental fitness is maximized by producing the greatest possible number of offspring that recruit into the territorial population and ultimately produce young themselves. If raising additional young reduces either the survivorship or future reproduction of their offspring, producing fewer young will increase parental fitness. In our study, survival probabilities, naive estimates of recruitment (proportion of juveniles observed as territory holders), and net reproductive value were all lower for juveniles that fledged in triplets than for those that fledged in pairs. One can evaluate the fitness consequences of producing three versus two offspring by multiplying parental reproductive output by (1) offspring recruitment probabilities and (2) the net reproductive value of juveniles. Fitness measured with both of these methods was slightly higher for parents that produced three offspring than for those that produced two, and fitness was more than 3× greater for parents that produced two or three young than for those that produced a single offspring (Fig. 5). Thus, although survival, recruitment, and net reproductive value were lower for juveniles that fledged in triplets (likely due to costs of reproduction), the additional offspring compensated for reduced offspring survival such that parents that fledged three young had a modest fitness advantage over parents that fledged two. Of course, our measure of parental fitness assumes that subsequent future reproductive success and survival are not affected by current reproduction. Although we did not evaluate life-history tradeoffs in parents here (this topic being the subject of a separate analysis), no relationship was detected between current and future reproduction in a large-scale study of Northern Spotted Owls (*S. o. caurina*; Forsman et al. 2011).

*Effect of life-history tradeoffs on assessments of territory quality.*—Indices of territory quality based on parental reproductive output must be robust to tradeoffs between parental reproductive output and offspring fitness if they are to adequately reflect the contribution of the territory to population growth. Specifically, indices based on parental reproductive output and measures of offspring fitness should be positively and linearly related, and the correlation between the two indices should be high. We expected that the index based on parental output might undervalue high-quality territories because parents on these territories would be more likely to fledge two or three than one young, and these young had higher relative fitness than predicted on the basis of parental reproductive output (Fig. 5). However, indices based on parental reproductive output and offspring fitness (offspring recruitment and net reproductive value) were significantly correlated, and relationships were linear (Fig. 4). We suspect that taking differences in the fitness of pairs or triplets into account had little effect

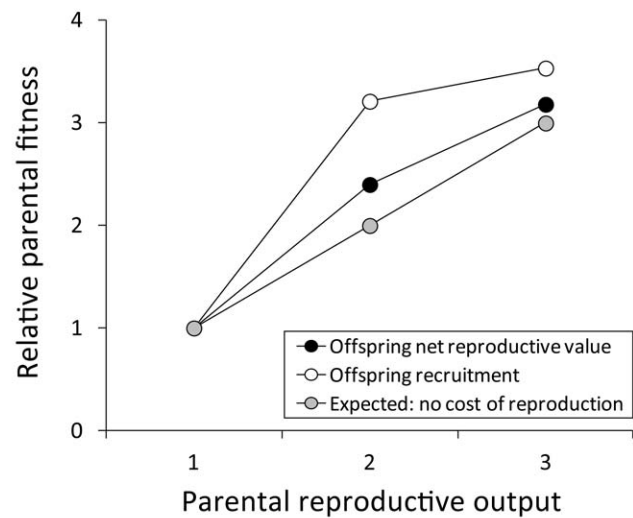


FIG. 5. Relative fitness of California Spotted Owl parents in the San Bernardino Mountains as a function of their reproductive output in a given breeding event, estimated on the basis of recruitment and net reproductive value of their offspring. Also shown is the expected fitness of parents under the assumption of no cost of reproduction to offspring.

on indices of territory quality because no young were produced in 496 of 878 (57%) observed breeding attempts, and a single offspring was the most common reproductive output when young were produced. Indeed, a single young was fledged more commonly in high- than in low-quality territories (23% vs. 15% in the lower vs. highest 50th percentile of territories, respectively) such that the fitness advantages of producing two or three offspring occurred too rarely to appreciably affect indices of territory quality.

The index of territory quality based on offspring recruitment was only moderately related to the index of territory quality based on parental reproductive output ( $R^2 = 0.23$ ), particularly compared with the strong relationship between the indices of territory quality based on offspring net reproductive value and parental reproductive output ( $R^2 = 0.99$ ; Fig. 4). We suspect that the relationship between recruitment and reproductive output was modest because an average of “only” 6.8 years of data was used to assess the quality of each territory. Moreover, the average number of recruits produced per territory was only 1.1, and 50 of 118 (42.4%) territories did not produce any recruits. Thus, territory-specific indices of quality based on recruitment were likely sensitive to the production of even a single recruit; as a result, stochastic events and sampling error in the index could have weakened its relationship with the index based on reproductive parental output. By contrast, the index based on net reproductive value was based on expected differences in fitness estimated at the population, rather than the territory, level and was presumably less affected by stochastic events that occurred at individual territories.

In sum, our results indicate that assessments of territory quality in Spotted Owls based on reproductive output provide a reasonable measure of the relative contribution of individual territories to population growth and are not seriously affected by life-history tradeoffs. This finding is important given that considerable resources have been invested in characterizing Spotted Owl habitat quality, in part with naive estimates of reproductive output in owl territories

(Franklin et al. 2000, Forsman et al. 2011). Moreover, using measures of offspring fitness to assess territory quality is not possible in many parts of the species' range because of high rates of dispersal by juveniles outside of study-area boundaries. The importance of rigorous estimates of territory quality is underscored by the profound effects that the management of Spotted Owl habitat can have on late-seral-stage forests and local economies (Simberloff 1987). However, Spotted Owl population growth rates are most sensitive to factors that influence adult survival (Noon and Biles 1990), and we did not evaluate tradeoffs between adult survival and other life-history traits. Moreover, the nature of tradeoffs depends critically on the life history of the species in question (Proaktor et al. 2007, Hamel et al. 2010), and the effects of tradeoffs between reproduction and juvenile survival could be stronger in other species. Thus, the generality of our findings should be evaluated for other life-history tradeoffs and in species with different life-history strategies.

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