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Implications of non-ideal occupancy for the measurement of territory quality

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ABSTRACT

Territory quality shapes population dynamics and has conservation implications for territorial species. Yet, quantifying territory quality using different measures can yield conflicting results, particularly if territory selection is non-ideal, thus challenging the understanding of territory quality. We used a 25-year population study of spotted owls (*Strix occidentalis*) occupying 72 territories to evaluate five commonly used demographic- and occupancy-based measures of territory quality: occupancy rate, annual apparent survival rate, territory fitness, mean annual reproductive rate, and total reproductive output. To do so, we evaluated pairwise relationships between measures of territory quality and assessed the extent to which spotted owls selected territories based on their potential to promote fitness. Measures of territory quality were generally positively correlated. Notably, however, territory occupancy explained less than half of the variation ($R^2 = 0.37$) in territory fitness (the expected fitness of territory holders). Non-ideal patterns in territory occupancy were the result of weak linkages between the likelihood of vacant territories becoming colonized and their fitness potential, particularly their capacity to promote reproduction. Imperfect territory colonization was likely the product of the spotted owl's strong site fidelity to even low-fitness territories and constraints on the ability of dispersing individuals to locate high quality territories. Mismatches emerging from non-ideal colonization have important conservation implications because populations may benefit more from habitat restoration at low fitness-high occupancy territories and more from conspecific attraction measures at high fitness-low occupancy territories. Our findings for spotted owls were reasonably consistent with broad patterns observed for other species in previous studies, but the strength of associations between pairs of territory quality measures often varied considerably, suggesting that species-specific assessments of patterns in territory quality are important. Finally, when practical, examination of the ecological processes shaping multiple measures of territory quality will benefit the study and conservation of territorial species.

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1. Introduction

Variation in territory quality shapes the population dynamics of territorial species (Brown, 1969; Newton, 1991; Rodenhouse et al., 1997). Individuals occupying high-quality territories can produce enough offspring to promote population growth, whereas individuals occupying lower quality territories typically produce fewer offspring—which can dampen population growth (Fryxell, 2001; Breininger and Carter, 2003; Pulliam, 1988; Brown and Kodric-Brown, 1977; Krebs, 1971). Moreover, variation in territory quality, coupled with the tendency of individuals to colonize higher quality territories when they become vacant, can exert negative density-dependent feedbacks that restrict population growth and have profound effects on population viability (Newton, 1998; Pulliam and Danielson, 1991; Rodenhouse et al., 1997). Thus, identifying high-quality territories that contribute disproportionately large numbers of potentially recruiting individuals can facilitate the prioritization of habitats and sites for management and conservation (Dias, 1996).

Territory quality is often assessed using demographic (reproductive and survival) rates given their linkages to individual success and population dynamics (Sergio et al., 2009; Low et al., 2010; Pärt et al., 2017). However, a lack of (or negative) correlation between different demographic rates of territory occupants could lead to misleading inferences of territory quality. Individuals that occur in presumed high-quality territories based on high reproductive rates, for example, may in fact contribute little to population growth if resource conditions that promote reproduction reduce survival (Reznick, 1985; Kristan, 2007) and because life-history trade-offs may occur between the two components of fitness (Dhondt, 2001). Consequently, "territory fitness," defined as the expected fitness of territory holders, has gained traction as a measure of territory quality because it integrates the two key components of fitness (reproductive and survival rates) into a single demographic-based measure (Franklin et al., 2000; Nystrand et al., 2010; Matthiopoulos et al., 2015). Territory fitness – the expected population growth rate of individuals on a territory – is a linear function of annual reproductive and survival rates and thus is expected to be correlated with both measures (Caswell, 2001). While territory fitness is mathematically most sensitive to survival rates in long-lived species (Noon and Biles, 1990), temporal variability in the measure can be shaped by reproduction (Franklin et al., 2000; Wisdom et al., 2000) such that a priori correlations are uncertain and could depend on the relative ability of individuals to assess cues promoting high survival versus reproduction. However, estimating territory fitness requires rigorous estimates of both stage-specific survival and reproductive rates, which can be impractical to obtain for certain species (e.g., cryptic, rare, and migratory species).

Challenges associated with estimating demographic measures, coupled with the advent of analytical approaches that account for imperfect detection (e.g., MacKenzie et al., 2003), have catalyzed the use of occupancy rates as a measure of territory quality (Sergio and Newton, 2003). The expectation is that higher-quality territories should be occupied for longer periods and more consistently relative to lower-quality territories (Johnson, 2007). However, individuals may not always occupy territories that confer high fitness or contribute large numbers of recruits to the broader population. Such non-ideal selection could occur for several reasons, including (i) imperfect knowledge of the location of high-quality territories in the landscape, (ii) a mismatch between cues used to assess territory quality that result in the use of low-quality territories (i.e., ecological traps), or (iii) very high site fidelity observed in some species which can lead to continuous occupancy of low-quality territories (Schlaepfer et al., 2002; Pagán et al., 2009). Thus, occupancy- and demographic-based measures of territory quality may exhibit different sensitivities to the life-history of the focal species and the manner in which each measure captures variation in the quality of territories likely depends on complex interactions between their mathematical properties and species life-history attributes such as the strength of site fidelity and the ability to assess ecological cues.

Because they can register different "signals" of territory-scale processes, occupancy- and demographic-based measures may lead to divergent assessments of not just relative territory quality, but also habitat quality and population dynamics that might suggest different conservation strategies. For example, conservation strategies effective for high fitness, low occupancy territories may not be effective for low fitness, high occupancy territories. Nevertheless, relatively few studies have explored processes shaping patterns of a suite of measures to territory quality or evaluated their implications for conservation planning owing, in part, to the challenges of collecting all the data required for such an analysis. However, we consider such an assessment timely in light of technological and analytical advances that increasingly facilitate the estimation of demographic- and occupancy-based measures of territory quality,

Table 1
Description of five commonly used measures of territory quality evaluated in this study.

Territory quality measure	Notation	Description	Relationship with other measures
Mean annual reproductive rate	M	The sum of young produced at a territory divided by total years, where years with no occupancy are treated as missing values	A component of total reproductive output
Total reproductive output	T	Total number of young produced by individuals occupying territory over the study period, where years with no occupancy are assigned a value of zero young produced	Effectively the product of the mean annual reproductive and the territory occupancy rates
Annual apparent survival	φ	The survival rate of individuals occupying a given territory for both adults and subadults	Component of territory fitness; expected to be positively associated with territory occupancy
Territory fitness	λ	The expected population growth rate of individuals occupying a territory	Estimated from a matrix parameterized by mean annual reproductive and territory survival rates
Territory occupancy rate	ψ	The proportion of years a territory is occupied	Expected to be positively associated with territory survival rate; a component of total reproductive output

even for elusive species (Roth and Amrhein, 2010; Thompson, 2013).

Here, we assessed the extent to which non-ideal territory selection may affect five measures of territory quality—annual reproductive rate, total reproductive output, annual territory survival rate, territory fitness, and territory occupancy rate (Table 1)—for spotted owls (*Strix occidentalis*) using data from a 25-year population study of this species. Specifically, we evaluated: (1) the degree to which demographic- and occupancy-based measures of territory quality were related; and (2) the extent to which any imperfect associations were due to non-ideal patterns of territory selection. The spotted owl is a useful species for this purpose because (i) it is highly territorial with individuals exhibiting strong interannual site fidelity (Carey and Peeler, 1995); (ii) individuals are easily detected in surveys; and (iii) detailed ecological studies have provided extensive information about territory quality. To meet these objectives, we evaluated pairwise relationships between measures of territory quality, assessed the extent to which spotted owls selected (i.e., colonized) vacant territories based on their potential to promote fitness, and explored occupancy and demographic histories at individual territories. Understanding when and why pairwise combinations of these measures are either tightly linked or decoupled may provide important insights into what processes are captured by individual measures of territory quality. Finally, we compared the strength of associations between pairs of territory quality measures to associations reported in previous studies of other species to evaluate the degree to which our results may be generalizable.

2. Methods

2.1. Spotted owl surveys

We surveyed 72 spotted owl territories located on our Eldorado study area (Jones et al., 2018) in the central Sierra Nevada, California from 1993 to 2017 using well-established protocols (Franklin et al., 1996). Thirty-nine of these territories occurred within a contiguous, demographic study area 355 km^2 in size, and 33 "satellite" territories occurred in the surrounding vicinity (Fig. 1). Briefly, we surveyed the entire contiguous area for spotted owls three to four times per year, conducting focal surveys at territories with a prior history of occupancy. Satellite territories were also surveyed three to four times per year, but only within approximately 2 km of previously detected nest and daytime roost sites. Occupancy status was determined by mimicking spotted owl calls to elicit responses and tracking owls back to nest and roost sites. Reproductive status was determined at occupied sites by offering live mice to territorial owls and recording the number of young observed (Franklin et al., 1996). We attempted to capture and band all spotted owls using the methods described in Franklin et al. (1996) where captured individuals were fitted with a U.S Geological Survey locking aluminum band on one leg and a unique combination of color band and tab on the other leg to facilitate identification by re-sighting; approximately 93% of all detected owls on the study area were banded each year (Berigan et al., 2019). We determined sex of territory occupants based on the sexually dimorphic pitch of their calls (Forsman et al., 1984), and determined age based on plumage characteristics and categorized birds as young-of-the-year (0-year old), first-year subadult (1-year old), second-year subadult (2-years old),

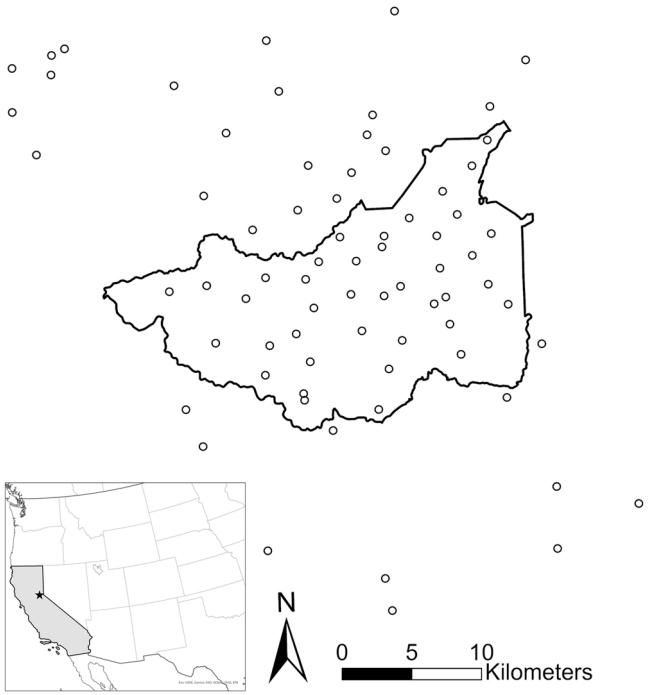

Fig. 1. Map showing study area and territories included in analyses. The demography study area is delineated by a black boundary. Black circles indicate territories within the study area that have been monitored since at least 1997.

and adult (>3-years old) (Forsman et al., 1984). For simplicity, we censored survey data in the years 2015–2017 at a total of 13 territories on our study area that experienced high-severity fire across > 50% of their ~400-ha territory area following a 2014 'megafire', and thus experienced a substantial change in quality (Tempel et al., 2014; Jones et al., 2016a).

2.2. Estimating territory occupancy and colonization rates

We used dynamic occupancy models applied to detection/non-detection data collected at the 72 spotted owl territories collected over our 25-year study period to estimate territory-specific occupancy (ψ_j) and colonization (γ_j) rates. We included only diurnal detections in our occupancy analysis because they better represented the presence of established resident and/or territorial individuals compared to nocturnal detections of wide-ranging individuals from nearby territories that yield upwardly biased estimates of occupancy (Berigan et al., 2019). A territory was considered occupied if either a single or pair of individuals was detected within the territory, and colonization was considered to have occurred if a single owl or pair of owls repatriated a known but previously unoccupied territory. Adopting these definitions allowed us to assess the likelihood of colonization based on the quality of the territory rather than, for example, the presence of a mate (i.e., a single owl).

We estimated temporally-averaged territory occupancy (ψ_j), or the proportion of years during the study period that each j territory was occupied corrected for imperfect detectability, using the implicit dynamics multi-season occupancy model within program PRESENCE version 11.5 (Hines, 2006). Typically this model is used to estimate seasonal occupancy, ψ_t (where the local extinction probability, ε, is constrained to $1-\gamma$, where γ is local colonization probability), but the design matrix can be constrained and structured with site-specific (territory) fixed effects that are time-constant such that the model yields the quantity of interest, ψ_j (J. Hines personal communication). In the detection (p) submodel, we used annual reproductive status (breeding or non-breeding) as a covariate because breeding owls are more easily detected (Jones et al., 2016b; Berigan et al., 2019).

We estimated territory-specific colonization rate (γ_j), using the standard explicit dynamics parameterization of a multi-season occupancy model with four parameters ($\psi_1, \gamma, \varepsilon, p$), where $\psi_1$was the initial occupancy probability, γ was the territory colonization probability, ε was the territory extinction probability, and p was the detection probability in program PRESENCE version 11.5. Similar to our above approach for obtaining ψ_j, we obtained the quantity γ_j by structuring the design matrix with site-specific (territory) fixed effects that were time-constant, holding ψ_1 and ε at their constant structures, and as above modeling p as a function of reproductive status.

2.3. Estimating mean annual reproductive rate and total reproductive output

We estimated the mean annual reproductive rate ($M_{j,a}$) of each territory j based on the number of young-of-the-year (which ranged from 0 to 3) produced at the territory by subadult and adult territory holders over the 25-year study. However, annual reproduction varies considerably in spotted owls based on environmental conditions (Franklin et al., 2000) such that mean annual reproductive rate could yield optimistic assessments of quality for territories that happened to be occupied in good reproductive years and pessimistic assessments for territories occupied in poor reproductive years. Accordingly, we calculated the mean annual reproductive rate for each territory based on the deviation in the number of young fledged in year k from the annual mean rather than the actual number of young fledged. Thus, mean annual reproductive rate M_j was calculated as $M_j = M_{j,k}$. We calculated $M_{j,k}$ as follows:

$$M_{j,k} = \frac{\left(\sum_{j=1}^{72} n_{j,k}\right)}{72} - n_{j,k},$$

Where $n_{j,k}$ is the number of young produced at territory j in year k. If the territory was not occupied (or was not surveyed) in year k, $n_{j,k}$ was treated as a missing observation. Standard errors for M_j were also calculated based from values of $M_{j,k}$ conditional on occupancy.

Because reproduction varies considerable between years for spotted owls, we measured total reproduction similarly to annual reproduction rates. We estimated the total reproductive output of subadults and adults occupying territory j (T_j) by summing the deviation in the number of young produced in each year k over the 25-year study (i.e., $\sum_{k=1}^{25} M_{j,k}$). However, in contrast to the estimate of M_j, $M_{j,k}$ was treated as 0 for territories confirmed to be unoccupied in year k and thus negatively impacted T_j. Moreover, because the number of years surveyed varied among territories, we scaled territory-specific estimates of total reproductive output as follows:

$$T_j = \frac{\left(\sum_{k=1}^{25} M_{j,k}\right)}{\left[\frac{(V_j)}{25}\right]}$$

V_j was the number of years territory j was surveyed which varied from 7 to 25 years. As such, the estimate of T_j was not influenced by years without surveys while providing a measure of territory quality that quantified the number of potential recruits provided by the territory to the spotted owl population. Standard errors for $T_j$were treated as zero given our previous studies suggest near perfect seasonal detection for young-of-the-year (Franklin et al., 2000).

2.4. Estimating annual territory survival rates

We used mark-recapture methods (Jolly, 1965) to estimate annual apparent survival rates for each territory j ($\varphi_{j,a}$), which reflected the joint survival rates of all subadult (1- and 2-year-old) and adult (≥3 years old) territory holders banded or resighted on a territory over the study. Subadults and adults, denoted a, were pooled for survival analyses because sample sizes were not sufficient to estimate stage-specific survival rates for each of the 72 territories. Young-of-the-year individuals were excluded because they do not typically defend territories and are rarely recaptured in subsequent years, presumably because of long natal dispersal distances out of the study area (Seamans et al., 2001). Capture histories represented the banding and resighting histories of individual owls but were grouped by territory to allow for the estimation of territory-specific survival rates. When an individual was observed switching to a new territory (i.e., made a breeding dispersal movement), we created a separate capture history starting in the first year it was detected on the new territory following Franklin et al. (2000). We did not censor the capture history of dispersing owls at the original territory because doing so would not have counted territory abandonment against territory survival as a measure of quality. We could not distinguish between dispersal and death for owls that moved outside of surveyed area (Fig. 1), but this limitation was not expected to affect territory survival rates because death and breeding dispersal have an equivalent effect on territory-specific survival rates. Thus, territory survival rates ($\varphi_{j,a}$) reflected the joint probability of subadults and adults surviving and remaining on a territory (j), which presumably would be high in high-quality territories. We estimated $\varphi_{j,a}$ using a model in which survival varied by territory and sex, treating each as a fixed effect, and recapture rate varied by sex in program MARK (White and Burnham, 1999). This model was > 2.0 AIC units lower than models where survival and/or p (capture rate) did not contain a sex covariate (Burnham and Anderson, 2002). This approach yielded time-averaged annual apparent survival rates; we did not test models in which survival varied among years for each territory because of sample size limitations. We found no evidence for lack of fit ($\hat{c} = 1.052$) ($\hat{c}$; Anderson et al., 1994) using the most highly parameterized model without a territory effect.

2.5. Estimating territory fitness

To estimate fitness for each territory j (λ_j), we used a two-stage class, female-based Leslie matrix (Caswell, 2001) containing young-of-the-year and subadult-adult territory holders (Franklin et al., 2000). We pooled subadults and adults in our model because we did not have sufficient data to estimate subadult and adult reproductive and survival rates separately for each territory and subadult only comprised a small fraction of total territory holders (7% male and 10% female) over the study period. Nevertheless, we expected territory-specific estimates of fitness to incorporate the effects of the age of territory holders given that subadults tend to have relatively low reproductive and survival rates (Seamans et al., 2001) and analyses of these two rates were done on a territory-by-territory basis. We parameterized the matrix with annual estimates of fecundity and survival rates for each territory as follows:

$$\begin{bmatrix} N_{y,t+1} \\ N_{a,t+1} \end{bmatrix} = \begin{bmatrix} 0 & \varphi_{j,a} m_{j,a} \\ \varphi_{j,y} & \varphi_{j,a} \end{bmatrix} \begin{bmatrix} N_{y,t} \\ N_{a,t} \end{bmatrix},$$

where N_y was the number of young in year t or $t+1$, N_a was the number of adults in year t or $t+1$, $m_{j,a}$ was the joint subadult-adult fecundity on territory j, $\varphi_{j,y}$ was the annual survival rate of young-of-the-year y on territory j, and $\varphi_{j,a}$was the joint female annual subadult-adult survival rate on territory j. We calculated fecundity (the number of female offspring produced per female in the population) by dividing territory-specific estimates of annual reproductive rates by two, assuming a 50:50 sex ratio for fledged offspring (Tempel et al., 2014). Standard errors associated with fecundity estimates were calculated using the delta method (Powell, 2007). We obtained territory-specific estimates of $\varphi_{j,a}$ from the best approximating model for survival described above. Reliable estimates of $\varphi_{j,y}$ for our study area were not available due to high dispersal and emigration rates of juveniles from our demographically open study areas. Therefore, we applied a common estimate $\varphi_{j,y}$ for each territory derived from an insular population of California spotted owls (i.e. $\varphi_{j,y} = 0.368$; LaHaye, 1988). We considered this approach adequate because population growth in spotted owls is relatively insensitive to variation in juvenile survival rate (Noon and Biles, 1990), and therefore would also be expected to contribute little to variation in territory fitness over long time periods. Territory fitness was estimated as the dominant, real eigenvalue of the two-stage class Leslie matrix. Standard errors associated with each territory-specific estimate of fitness were calculated with Monte Carlo simulations, where 1000 pairs of values for fecundity and survival rates were randomly generated from normal distributions with expected values and standard deviations set to estimates of $m_{j,a}$ and $\varphi_{j,a}$ and their respective standard errors (Alvarez-Buylla and Slatkin, 1994). Territory fitness was then calculated for each pair of simulated $m_{j,a}$ and $\varphi_{j,a}$ values and the standard deviation of the resultant 1000 values of territory fitness was treated as the standard error of the estimates of λ_j. This process was repeated for each territory j.

The aim of this study was to examine relationships between different measures of territory quality, not to evaluate the degree to which different environmental covariates explained variability in measures of territory quality. Previous research has exhaustively explored such questions, including the influence of forest structure (Jones et al., 2018; Tempel et al., 2014, 2016), fuel treatments (Tempel et al., 2015, 2014), wildfire (Jones et al., 2016a, 2021; Tempel et al., 2014) and climate (Jones et al., 2016b; LaHaye et al., 2004) on variation in occupancy and demographic rates. In addition, we did not include the presence of barred owls as a potential covariate for occupancy or colonization because barred owls were not established in the study area (Hofstadter et al., 2022).

2.6. Relating measures of territory quality

We assessed associations between all pairwise combinations of the five measures to understand how each measure captured aspects of territory quality. Specifically, we tested for relationships between pairs of measures using linear regression analysis, designating the dependent variable in each regression as the measure more likely to be influenced by the second measure (i.e., independent variable in the regression model). For example, because territory fitness was calculated as a direct function of mean annual reproductive and survival rates, it was always treated as the dependent variable in regression analyses involving reproduction and survival. The coefficient of determination R^2 was estimated for each pairwise combination of territory quality measures to assess the extent to which measures were decoupled by non-ideal territory selection (see also below). To show that we estimated between-territory variation in territory quality rather than variation in measures of quality, we compared the observed range of variation in territory fitness to a realistic null model in which all territories were equal. Pairwise comparisons with null model estimates yielded far weaker relationships than comparisons with our original estimates of territory fitness (Appendix B).

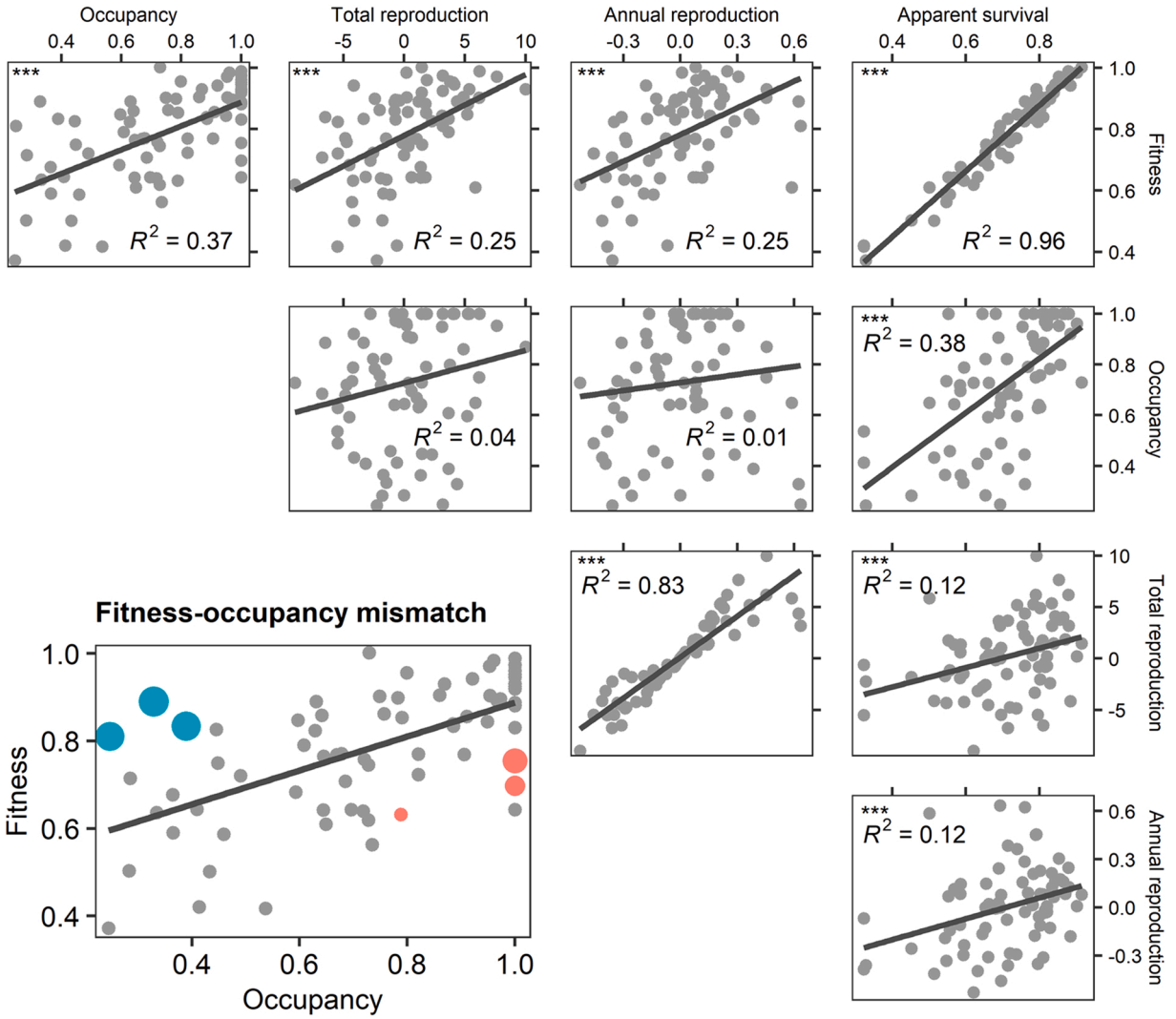

Fig. 2. Scatterplot matrix showing pairwise relationships among five measures of territory quality for 72 spotted owl territories. Each plot in the matrix indicates the best fitted relationship between two demographic measures. Number of asterisks represent the level of significance where *** $= p < 0.001$, ** $= p < 0.01$, and * $= p < 0.05$. Light blue and red dots in the inset plot represent subjectively selected territories that demonstrate a high degree of mismatch between territory occupancy and fitness. The size of these light blue and red circles (drawn to scale) indicates the total number of young fledged by territories. Histograms along the diagonal represent frequency distributions for each of the five measures of territory quality. Normality plots and residuals are available in Appendix D and Appendix E.

2.7. Testing for ideal vs non-ideal territory selection

We tested for ideal versus non-ideal patterns of territory selection by relating the probability of each territory j becoming colonized (γ_j), conditional on vacancy, to the: (1) mean annual reproductive rate ($M_{j,a}$), (2) the territory survival rate, and (3) territory fitness (λ_j) of territory j. The expectation was that high-fitness territories would have high probabilities of colonization if territory selection was ideal (i.e., individual owls were able to effectively locate and assess vacant territories with the potential to promote high survival and reproductive rates). By contrast, the association between colonization and fitness would be weak or non-existent if territory selection was non-ideal. We limited this analysis to estimating the correlation between territory colonization and the mean annual reproductive rate, territory survival, and territory fitness because these three measures are conditional on occupancy and thus mathematically unrelated to colonization. In other words, any association between territory colonization and these three measures was expected to be the result of preferential selection by owls. By contrast, colonization was expected to be related to total reproductive output even in the absence of preferential selection because colonization increases occupancy and thus potentially the number of young produced at the territory.

2.8. Comparing associations between measures to previous studies

To evaluate the extent to which our results may be generalizable, we compared the strength of association between pairs of territory quality measures in spotted owls to the same measures estimated for other species in previously published papers. To do so, we reviewed papers published in ecological journals up to December 2019 using the Google Scholar search engine. We used the following terms: “territory quality”, “territory fitness”, “annual survival”, “total reproductive output”, “reproductive rate”, and “occupancy”. We also searched for synonyms: “lifetime reproductive output” for “total reproductive output”, “annual productivity” for “annual reproductive rate” and “breeding habitat quality” for “territory quality”. We used the Boolean operators “AND” to combine search terms and “OR” to include multiple search terms, and synonyms and terms were hemmed in quotations to ensure that exact phrases were searched. Our searching strategy resulted in the following structure: “territory quality” AND ("territory fitness" OR "annual survival" OR "annual productivity" OR "total reproductive output" OR "lifetime reproductive output" OR "reproductive rate" OR "annual productivity" OR "occupancy rate"). We repeated the search by substituting “territory quality” with its synonym “breeding habitat quality” because including it in the initial search would have resulted in an overly complex search structure and a prohibitive number of articles to review. Although other databases could also be searched, our search of Google Scholar alone yielded 1537 articles that we considered robust enough to place our study in the context of previous studies. When correlation coefficients were reported separately for males and females in the same study, or for the same species occupying different sites in the same study (e.g., Carrete et al., 2006, Krüger et al., 2012), we calculated the mean of reported values since individual values were unlikely to be independent. We excluded articles that did not report R^2 values for the pairwise measure considered in this study. We included studies that did not censor encounter histories when individuals switched territories in survival analysis (see description above), because territory-specific estimates for spotted owls with/without censoring were almost perfectly correlated ($R^2 = 0.99$), and excluding these studies would have resulted in small sample sizes. No previous study that we encountered used deviations from annual means when calculating reproductive measures of territory quality; as such, we used values for the mean reproductive rate and total reproductive output that were uncorrected for annual variation in reproductive success when comparing R^2 values between our and previous studies.

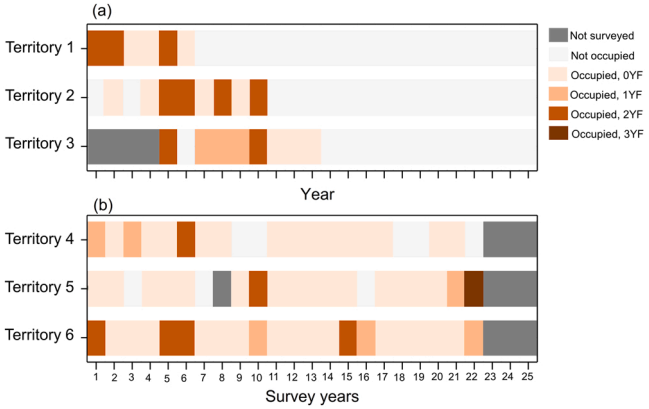

Fig. 3. Mismatch between territory fitness and occupancy. Patterns of mismatch are shown between territory fitness and occupancy rates in (A) three spotted owl territories exhibiting high territory fitness and a low territory occupancy rates, and (B) three territories exhibiting low territory fitness and a high occupancy rate. YF represent the number of juvenile spotted owl fledged each year when a territory was occupied.

3. Results

3.1. Measures of territory quality

Estimates of quality were variable among territories, with total reproductive output exhibiting the most variation and annual territory survival and territory fitness exhibiting the least variation based on coefficients of variation (Appendix A). The most precisely estimated measure was territory occupancy and the least precisely estimated measure was the mean annual reproductive rate (Appendix A).

The mean annual reproductive rate was positively related to total reproductive output ($R^2 = 0.83$) indicating that territories whose occupants had high reproductive success on an annual basis also tended to produce more young over the study period (Fig. 2). The mean annual reproductive rate and total reproductive output were both significantly but weakly related to the annual apparent survival rate (both R^2's = 0.12; Fig. 2). Territory fitness was significantly, positively, and strongly related to annual apparent survival rate ($R^2 = 0.96$) but only modestly associated with total reproductive output ($R^2 = 0.25$; Fig. 2). The association between territory fitness and the annual reproductive rate was positive but modest as well ($R^2 = 0.25$).

Territory fitness and territory occupancy were significantly and positively related, but the strength of the relationship was modest ($R^2 = 0.37$) and the fitness of some territories deviated considerably from expectations based on occupancy (Fig. 2). Examination of the naïve occupancy and demographic histories of individual territories that exhibited both (1) high fitness and low occupancy and (2) low fitness and high occupancy (blue and red symbols in Fig. 2) provided insights into reasons for mismatches between the two metrics. High fitness-low occupancy territories were often occupied for only a small portion of the study but, when occupied, territory holders frequently produced young (Fig. 3A). In contrast, low fitness-high occupancy territories were occupied for much of the study but were frequently non-reproductive (Fig. 3B). As a consequence, total reproductive output could be low at both high-fitness and high-occupancy territories (see enlarged panel in Fig. 2) and was very weakly associated with territory occupancy ($R^2 = 0.04$) and only moderately associated with fitness ($R^2 = 0.25$, as above). Occupancy was significantly and positively associated with the annual apparent survival rate ($R^2 = 0.38$) and was not associated with annual reproductive rate ($R^2 = 0.01$; Fig. 2).

3.2. Testing for non-ideal territory selection

The probability of an unoccupied territory becoming colonized by a single or pair of owls was inestimable for six of the 72 territories that were occupied in all years they were surveyed, and these observations were therefore excluded from tests of non-ideal territory selection. Vacant territories were more likely to be colonized by a single or pair of spotted owls if fitness and survival were higher at the territory ($p < 0.01$ for both tests), but the amount of variation in territory colonization explained by territory fitness was relatively weak ($R^2 = 0.16$; Fig. 4A). Vacant territories tended to have higher colonialization probabilities when the mean annual reproductive rate was higher, but the relationship was not significant ($p = 0.07$) and the amount of variation in territory colonization explained by the mean annual reproductive rate was low ($R^2 = 0.05$; Fig. 4B). The amount of variation in territory colonization explained by survival was low (0.14; Fig. 4C).

3.3. Comparison with previous studies

Our literature search yielded 1537 published articles which, upon review, included 29 studies involving 26 species, all birds, that presented 44 estimates of R^2 values for pairs of territory quality measures (Appendix F). The strengths of associations between pairs of

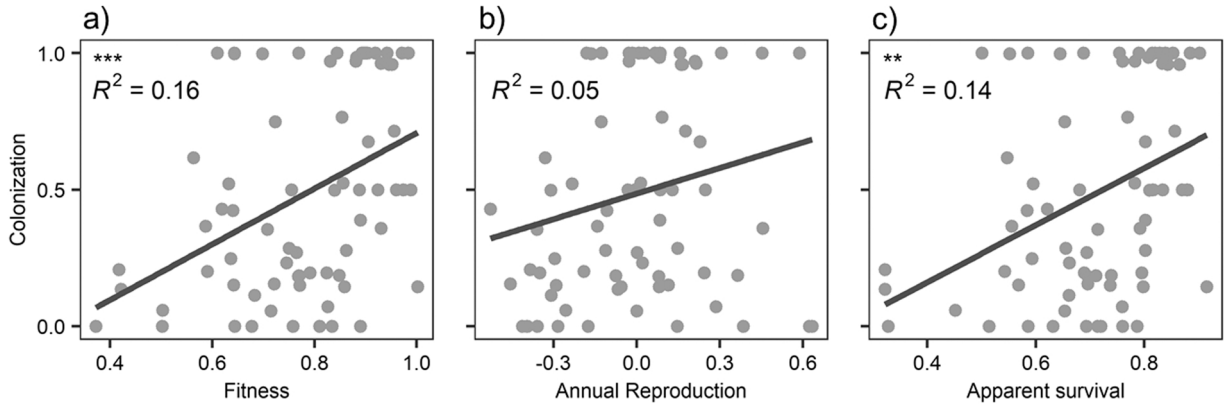

Fig. 4. Colonization and territory quality estimates. Pairwise relationships are shown between territory colonization (γ) and territory quality estimates (fitness: λ_j; annual reproduction: $M_{j,a}$; apparent survival: $\varphi_{j,a}$) for 66 spotted owl territories over 25 years. Each plot indicates the best fitted linear relationship between demographic measures. Number of asterisks represent the level of significance where *** = $p < 0.001$, ** = $p < 0.01$, and * = $p < 0.05$.

territory quality measures (i.e., R^2 values) estimated in this study were, in most cases, reasonably similar to mean values estimated by previous studies (Fig. 5); specifically, differences in R^2 values estimated for spotted owls and the mean of previous studies ranged from < 0.01–0.25. The greatest discrepancy occurred for the mean annual reproductive and apparent survival, which were only weakly correlated in spotted owls ($R^2 = 0.12$), but on average more strongly associated in other species ($R^2 = 0.38$). However, R^2 values for several pairs of measures of territory quality varied considerably across studies, most notably total reproductive output and territory occupancy, for which R^2 ranged from 0.004 to 0.92.

4. Discussion

Leveraging a multi-decadal study on the demography and territory occupancy of spotted owls, we found that commonly used measures of territory quality were positively associated. Positive correlations between pairs of territory quality measures were an a priori expectation to the degree that ecological conditions at high quality territories benefit multiple aspects of life history, such as reproduction and survival, and promote high site fidelity. This finding is encouraging because, when only a single measure of territory quality (e.g., occupancy rate) can be estimated, it may capture some of the ecological processes registered by several other measures. However, correlations between pairs of measures were imperfect with no statistical association between territory occupancy and the mean annual reproductive rate (Fig. 2). As such, our results also indicate that individual measures can capture different ecological processes affecting individual performance and territory dynamics, and thus do not necessarily capture the full suite of processes that determine the value of a site to the population. Thus, despite their frequent use, our study illustrated that—in some cases—assessing territory quality based on a single measure could potentially yield incomplete information about the relative value of sites. By evaluating pairwise relationships among these measures, we were able to identify some of the ecological processes captured by individual measures that provide insights as to how they can be integrated to assess territory quality more rigorously, acknowledging that our assessments of territory quality were made agnostic of the quality of individuals occupying those territory (see below).

The modest association between the mean annual reproductive and territory survival rates ($R^2 = 0.12$) suggests that individual reproductive and mortality processes can respond to environmental conditions differently. In spotted owls, survival can be associated more with the prevalence of older forests whereas reproduction can be more dependent on the juxtaposition of younger and older forests within territories (Franklin et al., 2000). Vital rates may also be decoupled as a result of life-history trade-offs, especially in long-lived species where reproductive effort comes at a cost to survival (Congdon et al., 1994; Hyslop et al., 2012; Tack and Noon, 2017; Stoelting et al., 2014; Peery and Gutiérrez, 2013). Thus, assessments of territory quality based on annual reproductive rates may produce different conclusions than evaluations based on annual apparent survival rates. Territory fitness integrates annual reproductive and survival rates and is thus more likely to reflect the response of territory holders to the suite of ecological factors (e.g., resources, predation risk, and local climate) that determine quality of territories than either measure alone (Franklin et al., 2000). Nevertheless, territory fitness was almost perfectly correlated with annual apparent survival rates, whereas fitness and annual reproductive rates were weakly correlated by comparison. These findings are consistent with life history strategies of long-lived species, in which fitness is less sensitive to reproduction and more sensitive to adult survival (Seamans and Gutiérrez, 2007b; Sergio et al., 2011; Griesser et al., 2017; Öst et al., 2018). As such, annual apparent survival rates are likely to be more robust measures of territory quality than annual reproductive rates for long-lived species when one of the two can be estimated. Moreover, in such cases,

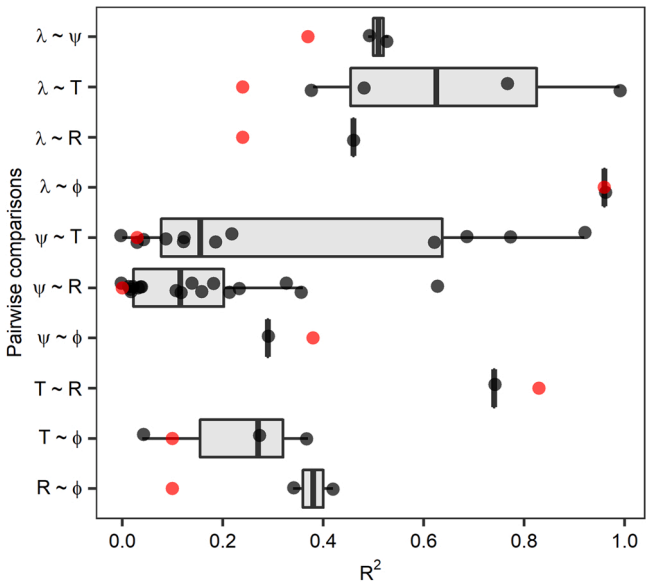

Fig. 5. Comparisons with previous studies. Strength of relationships (R^2 values) between pairwise combinations of individual measures of territory quality for spotted owls in our study (red) and other published studies that estimated and related measure of territory quality (gray).

estimates of annual apparent survival rates may be nearly synonymous with apparent fitness given the almost perfect correlation between these two measures.

The positive association between territory fitness and occupancy rates we observed indicated that spotted owls preferentially occupied high-quality territories that exhibited a tendency to promote their fitness. Indeed, variation in occupancy rates among territories is expected to reflect differences in territory quality—particularly in territorial species conforming to an ideal despotic distribution model (Zimmerman et al., 2003). Accordingly, it is often assumed that occupancy rates are a reasonable surrogate for the fitness of territory holders (Sergio and Newton, 2003). However, fitness explained less than half of the variation ($R^2 = 0.37$) in territory occupancy, suggesting imperfect (i.e., non-ideal) patterns of territory occupancy in spotted owls. Mismatches occurred because several territories with high fitness had low occupancy rates and several territories with low fitness had high occupancy rates (Fig. 3). Non-ideal patterns of territory occupancy were, in part, the result of territory colonization being unrelated to the mean annual reproductive rate (Fig. 4B)—i.e., the reproductive potential of territories (indeed, occupancy and reproductive measures were uncorrelated). While a statistically significant positive association between territory fitness and territory colonization indicated that high-fitness territories tended to be more likely to become colonized than low-quality territories when unoccupied, territory fitness explained little of the variation in territory colonization (Fig. 4A). The correlation between territory survival and colonization (Fig. 4C) suggested that spotted owls selected territories based on their ability to support survival rather than reproduction—as expected in long-lived species with a bet-hedging life-history strategy (Franklin et al., 2000). Nevertheless, non-ideal patterns of territory selection and settlement, to a degree, appeared to decouple territory fitness- and occupancy-based measures of territory quality in this species.

Non-ideal patterns of territory colonization could occur for several reasons. Strong site fidelity in territorial spotted owls limits the extent to which individuals will move to higher-quality territories and leads to the extended occupancy of relatively low-quality territories (Blakesley et al., 2005; Seamans and Gutiérrez, 2007a). Imperfect knowledge of territory quality could create non-ideal occupancy patterns because cues are not available, are masked by environmental stochasticity, or are maladaptive (Flesch, 2017). Moreover, constraints and risks associated with dispersal and the colonization of high-quality territories may cause some territories to be occupied more or less than expected based on their fitness benefits (Morris, 1987; Seamans and Gutiérrez, 2006). Finally, variation in territory occupancy and fitness patterns can be a function of quality of the individual territory holders, and the presence of low-quality individuals on higher-quality territories could obscure expected occupancy-fitness relationships (Zabala and Zuberogoitia, 2014). Inexperienced subadults, for instance, may have opportunities to occupy higher quality territories when they become vacant and, indeed, 27% of all male territory colonizers and 18% of all female territory colonizers in our study were subadults. Additionally, a higher quality individual on a lower quality site might express intermediate levels of territory fitness but relatively high occupancy. However, disentangling the effect of individual and territory variation quantitatively is challenging in long-lived species with high site fidelity such as spotted owls because most individuals only occur on a single territory and many territories were only occupied by a single or small number of different pairs of owls.

The degree of mismatch between territory fitness and occupancy emerging from non-ideal colonization has important conservation implications and may be more informative than either territory fitness or occupancy alone. High fitness-high occupancy territories are likely the most important to population viability given they are expected to produce large numbers of young and thus potential recruits. Accordingly, prioritizing the protection of such territories, for example from habitat loss or degradation, is expected to yield relatively high conservation benefits. By contrast, habitat restoration that improves the fitness of territory holders may be a more suitable strategy at low fitness-high occupancy territories and may yield population level benefits. Increasing territory-scale heterogeneity, and thus more edge habitat that facilitates resource acquisition, may increase spotted owl fitness in highly occupied territories that are generally less productive (Tempel et al., 2014). Such approaches seem particularly likely to be successful given that these territories are often occupied, with residents expected to realize the benefits of improved habitat conditions. Applying con-specific attraction measures at high fitness-low occupancy territories seem more likely to improve the status of imperiled populations than protection or restoration strategies. Indeed, attracting non-territorial individuals or individuals from lower quality sites to high fitness territories that are rarely occupied by, for example broadcasting con-specific cues, has proven to benefit several species of concern (Andrews et al., 2015; Farrell et al., 2012; Fletcher, 2006). Low fitness-low occupancy territories might require a combination of conservation measures to realize population gains and may be of lower priority for conservation that other territories, acknowledging that the restoration of habitat and individuals at such territories could be needed to ensure the viability for particularly imperiled populations.

Estimating territory fitness or occupancy may not be practical for some species, for example because of constraints on the ability to estimate survival rates with mark-recapture approaches or ability to survey territories in multiple occasions within years (needed to estimate detection and thus occupancy). Without territory fitness information, territories with high occupancy rates may seem like logical choices for protection yet may produce few young if fitness is low (see small red circular symbols in the inset of Fig. 2, Fig. 3B). Conversely, without territory occupancy information, territories with high fitness may seem like logical targets for protection yet may also produce few young because, as described above, estimates of territory fitness are insensitive to territory vacancies (see small blue circular symbol in the inset of Fig. 2, Fig. 3A). Thus, protecting either type of territory (in the absence of, for example, habitat restoration or social attraction measures) may not yield the expected population benefits. In such cases, total reproductive output may provide useful insights into the relative recent value of individual territories to the broader population as it reflects the total number of potential recruits produced. Nevertheless, the most useful measures will likely depend on species life history and practical issues pertaining to the feasibility of estimating each measure.

5. Conclusion

Similarities in the strength of associations between specific pairs of measures of territory quality estimated for spotted owls and the same pairs of measures estimated for other species would suggest that our findings are generalizable and could guide the estimation of territory quality more broadly. While our estimates of R^2 for pairs of measures were generally similar to mean R^2 values estimated across studies of other species, variability in the strength of association was often high among species (Fig. 5). This observation suggests that ecological processes that shape patterns of demography and occupancy vary considerably among species. Certainly, some variability in the strength of association between territory quality measures among species could be attributed to differences in life history strategies such as lifespan and degree of territory fidelity among species. For example, R^2 values for territory occupancy and the mean annual reproductive rate in song sparrows (0.64; Germain et al., 2018) and for total reproductive output and territory survival in red-billed choughs (0.02; Reid et al., 2006) could be considered outliers, both species being relatively short-lived. However, variability in R^2 values remained high for several pairs of territory quality measures when only relatively long-lived species were considered; for example, R^2 values ranged from < 0.01–0.92 for the association between total reproductive output and territory occupancy. Thus, thoroughly understanding the processes governing demography and occupancy at the territory scale, and ultimately quantifying territory quality for conservation purposes, could require the estimation of multiple measures of territory quality for a focal species of interest.

Characterizing variation in territory quality is an important precursor to understanding the processes that drive population change and ensuring effective conservation of territorial species. Here, we demonstrated that the scientific basis for identifying high-quality territories is strengthened by an improved understanding of the performance of individual and combined measures of territory quality. Indeed, as such assessments are dependent on limited resources for ecological research and conservation action, the use of suitable tools that reliably identify the underlying drivers of territory quality could help assure that limited resources are not wrongly invested in protecting less optimal territories or sink habitats.

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Ethics statement

All research was carried out under required federal and state permits, including the State of California Department of Fish and Wildlife Scientific Collecting Permit #SC-2114. Survey and handling procedures were reviewed and approved by the Animal Care and Use committees of the University of Wisconsin-Madison under IACUC A005367-R01.

Authorship contribution statement

FA and ZP conceived the ideas and designed methodology. **SW and WB** collected the data. **BH, GJ, KM, and DT** contributed to occupancy and demographic calculations and analyses. **KM and GJ** constructed the manuscript and handled reanalysis. All authors contributed to writing drafts and gave final approval for publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02097.

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