

Empirical support for a despotic distribution in a California spotted owl population

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Territorial species, such as the spotted owl (*Strix occidentalis*), are predicted to follow an ideal despotic distribution. However, debate exists on whether wild populations actually meet the assumptions of an ideal distribution, such as perfect perceptual abilities (i.e., the ability to recognize high- and low-quality sites without error). Because this hypothesis has important life history ramifications for spotted owls, we investigated whether occupancy rates of California spotted owl (*S. o. occidentalis*) territories in the San Bernardino Mountains of southern California positively correlated with a qualitative “potential fitness” (denoted by λ_{pf}) estimated from survival and reproduction of territorial owls. Spotted owls in our study tended to occupy territories with the highest λ_{pf} , supporting the assumption of ideal perceptual abilities within this population. However, this relationship was noisy, and we suggest that some individuals do not assess site quality accurately because of perceptual limitations, prey dynamics, and large territory sizes. Furthermore, dispersal processes, high survival rates, and long life spans of spotted owls may be other key factors preventing some individuals from selecting sites of the highest quality and, consequently, our ability to precisely estimate λ_{pf} . *Key words*: California, California spotted owls, fitness, ideal despotic distribution, *Strix occidentalis occidentalis*, territory occupancy. [*Behav Ecol* 14:433–437 (2003)]

Understanding mechanisms controlling spatial distributions of animals is critical to the conservation and management of wildlife (Kennedy and Gray, 1993). The ideal free distribution (IFD) and ideal despotic distribution (IDD) are models describing distribution patterns of wildlife populations (Fretwell, 1972). The IFD assumes that individuals will occupy the best sites until, due to crowding effects, average fitness within that habitat declines to equal that in the next best habitat type. Territorial behavior could alter this pattern (Fretwell and Lucas, 1969), which led Fretwell (1972) to formalize the IDD. The IDD model assumes that dominant individuals occupy the best sites, forcing the subdominant individuals to use lower quality sites (Fretwell, 1972). As with all hypotheses in ecology, the IFD and IDD are based on critical assumptions, including an animal’s perfect knowledge of available resources. Since their formalization, ecologists have modified the IFD and IDD models in an attempt to address these assumptions, which has improved our ability to predict the spatial distribution of individuals (Tregenza, 1995).

The assumptions that individuals have perfect knowledge of habitat quality, that habitats vary in their suitability, and that individuals incur higher fitness by occupying sites with the most available resources are critical components of both the IFD and IDD (Bernstein et al., 1991; Block and Brennan, 1993; Fretwell and Lucas, 1969; Rodenhouse et al., 1997). Fretwell and Lucas (1969) labeled organisms that maximize survival and reproduction by selecting quality habitats “ideal.” They argued that this assumption is valid because ideal individuals are favored through natural selection. However, others contend that this assumption is unrealistic due to perceptual constraints or imperfect knowledge of resources (Gray and Kennedy, 1994; Pyke et al., 1977; Rapport, 1991).

One study of the northern spotted owl (*Strix occidentalis caurina*), a territorial species, concluded that the owls followed an IDD (Franklin et al., 2000). We have studied the population dynamics and territory occupancy of California spotted owls (*S. o. occidentalis*) in southern California for 12 years. Some owls settled in areas where they did not reproduce, yet they remained on the unproductive territory. This led us to question the adaptive value of occupying territories that did not confer reproductive potential. Therefore, we investigated whether occupancy rates of spotted owl territories reflected potential fitness (*sensu* Franklin et al., 2000; see definition below) of those territories. Our goal was to add to the work of Franklin et al. (2000) by exploring whether our field data supported an IDD in another spotted owl population. In addition, we used an analytical technique that incorporated both survival and fecundity into a single fitness estimate to explore the validity of the ideal assumption for this population.

METHODS

Study area

Our study area was approximately 140 km east of Los Angeles, California, USA (34°15' N; 117°55' E) in the San Bernardino Mountains. This range is oriented east/west with elevations ranging from 800 to 3500 m and is surrounded by desert and chaparral vegetation (Vasek and Barbour, 1988). The climate is Mediterranean, with most precipitation occurring during the winter in the form of snow above 2000 m and rain at lower elevations. Annual precipitation ranges from 25 to 100 cm and varies with elevation and slope aspect (Minnich et al., 1995). Vegetation grades from Mojave desert scrub and southern coastal scrub at lower elevations to alpine at the highest elevations (Minnich, 1998). Within this continuum, local aspect and topography formed a complex mosaic of forest, chaparral, desert, and wetland vegetation patches. The mountain range was surrounded by vegetation unsuitable for spotted owls (LaHaye et al., 2001); therefore, the population was insular.

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Field techniques

In 1989, we began a long-term demographic study of California spotted owls in the San Bernardino Mountains. We annually surveyed all previously occupied spotted owl locations and all forest vegetation that could potentially support spotted owls, which included the entire mountain range from 1989 to 1998. We conducted surveys at night by imitating spotted owl vocalizations for a minimum of 15 min at call points or by calling continuously along designated survey routes (Forsman, 1983). These call points were strategically placed to cover forested vegetation types. For example, we did not establish survey points in areas of desert or chaparral because California spotted owls require at least some forested habitat (Gutiérrez et al., 1992). Therefore, the distribution of survey points reflected the distribution of forests and were not evenly spaced across the landscape. In addition, the number of survey points for each area varied due to landscape features, distribution of forest, and access. Upon receiving a response, we recorded the spotted owl's gender and then attempted to visually locate the bird. Once located, we attempted to capture and band all spotted owls. We placed a locking aluminum band on one leg and a unique combination of plastic color band and colored vinyl tab on the other leg (Franklin et al., 1996). In addition, we attempted to evaluate each owl's social status (paired, single) and estimate its reproductive effort (Franklin et al., 1996). We conducted surveys, capture, and identification of individuals during each breeding season (April–August). If owls were not located at a particular site after three complete surveys within a field season, we classified the territory (previously occupied site) or survey (previously unoccupied, but potential habitat) as vacant for that year.

Specific methods for estimating occupancy and potential fitness

We calculated occupancy rates of individual spotted owl territories as the proportion of years that a territory was occupied by a pair of owls. For example, a site that was occupied by a pair 3 of 10 years had an occupancy rate of 0.30. If we did not conduct a minimum of three surveys in an area within a year, we considered the occupancy of that area for that year as unknown and coded it as missing data. Although we attempted to survey all potential habitats, we did not conduct a complete census of spotted owls in the study area. Further, our estimates of occupancy may have underestimated true occupancy rates because we did not know whether territories without an owl response were unoccupied or if the owls simply did not respond. However, we believe that any bias in occupancy estimates was small because our surveys were designed to maximize detection rates (Reid et al., 1999), and resighting rates of spotted owls using these survey methods are known to be high (Seamans et al., 2001). Areas that were known to contain owls before our study but that were not occupied during our study (i.e., territories with occupancy rates of zero) were not included in our analysis.

Because fitness was a trait of individual organisms, territories could not exhibit fitness (Franklin et al., 2000). Therefore, we calculated a potential fitness value (λ_{PF}) for each territory from estimates of survival and fecundity of owls that occupied those territories. We calculated λ_{PF} by incorporating estimates of apparent survival of male and female owls on each territory and estimates of mean annual fecundity of females on each territory into a 3×3 Leslie matrix (Franklin et al., 2000) by territory. We then calculated λ_{PF} as the dominant eigenvalue of the Leslie matrix through matrix eigenanalysis (Danchin et al., 1995; Franklin et al., 2000). This value represented a λ_{PF} that

could be expected for owls occupying that territory. We assumed that λ_{PF} was influenced by unmeasured attributes of that territory (e.g., prey availability, habitat quality). Thus, the λ_{PF} estimate represented a relative measure of quality among territories such that owls occupying territories with a higher λ_{PF} would be expected to have the potential for a higher combination of survival and fecundity (fitness) than owls occupying territories having a lower λ_{PF} .

Our estimates of λ_{PF} had large standard errors because in most cases we had very few repetitions (individual birds) per sampling unit (territory) to estimate apparent survival. These large standard errors indicated that the λ_{PF} estimates were not precise. By using imprecise estimates as continuous variables, we would have implied overly optimistic confidence in our estimates of λ_{PF} . Therefore, we converted continuous λ_{PF} estimates to a categorical binary response variable with two categories (high and low) to investigate general trends between occupancy and λ_{PF} . We converted the λ_{PF} estimates to a binary variable (denoted as λ_{PF}) based on biologically meaningful principles rather than statistical principles. Specifically, we assigned territories with estimates of $\lambda_{PF} \geq 1$ into a high-quality group where females were more likely to replace themselves. Thus, these territories were assigned a 1 to represent a success. Territories with λ_{PF} estimates < 1 were assigned a 0 and represented sites where females were less likely to produce enough offspring to replace themselves.

We estimated apparent survival of owls on individual territories with a matrix of individual capture histories using the program MARK (White and Burnham, 1999). These estimates could have been biased if dispersal rates from the study area were high. However, field data on dispersal indicated that immigration and emigration rates for this population were low if they occurred at all (LaHaye et al., 2001). Previous survival models for this population indicated that gender did not influence survival estimates (LaHaye et al., 1994). Therefore, we did not include gender effects when modeling survival. Our estimates of λ_{PF} incorporated survival estimates of territorial adults and subadults only. Previous modeling indicated annual survival rates varied between adults and subadults (LaHaye, unpublished data). However, the number of territorial subadults in the population was so small relative to adults that we excluded age effects from survival models. We assumed that the probability of recapture was constant among territories. Apparent survival estimates for each territory represented the mean annual probability of survival for male and female spotted owls that occupied that territory. Owls moving among territories could have artificially reduced apparent survival estimates. We accounted for the movement of owls among territories by considering them "losses on capture" (Franklin et al., 2000; Jolly, 1965). Thus, owls that moved among territories were removed from the analysis on the original territories once they moved, rather than treating them as deaths. These individuals were then included in the analysis for the new territories.

We defined fecundity as the number of female young fledged per territorial female. We used mixed modeling (Proc Mixed: SAS Institute, 2000; see also Littell et al., 1996) with a repeated-measures design to model fecundity. Territory was the sampling unit, and years were repeated within territories. We considered territory a random effect because we probably did not detect all members of the population even though we surveyed all potential owl habitat in the study area every year. Therefore, we technically monitored a sample of the spotted owl population in the San Bernardino Mountains.

We assessed normality with normal probability plots and the assumption of constant variance with a modified Levene test (Neter et al., 1996). These tests indicated non-normality and nonconstant variance in our fecundity data. Therefore, we

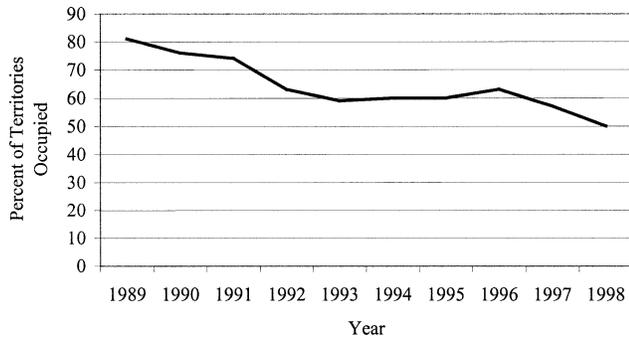


Figure 1

Annual occupancy rates of 128 California spotted owl territories in the San Bernardino Mountains, California, from 1989 to 1998.

used a normal-based mixed-model analysis to estimate fecundity because it was more robust to departures from the assumptions of normality and constant variance than non-linear models were to departures from their assumed distributions for count data (White and Bennetts, 1996). Further, mixed modeling allowed the error variance matrix to be structured for nonconstant sampling variances among years (Franklin et al., 2000) using the global model (Burnham and Anderson, 1998) and restricted maximum likelihood (Littell et al., 1996). We compared compound symmetric, autoregressive, and standard variance components covariance structures (Littell et al., 1996). Covariance structures were ranked by their ability to fit the data with a small sample size adjustment of Akaike's information criterion (AIC_c ; Hurvich and Tsai, 1989; Burnham and Anderson, 1998). We used standard maximum likelihood and the highest ranked covariance structure to estimate territory-specific fecundity. Similar to survival, we eliminated age effects in modeling fecundity because we had few repetitions per territory. Final estimates represented the mean annual fecundity of the females on that territory during the years that the territory was occupied and that reproduction could be assessed.

After estimating an occupancy rate and λ_{pf} for each territory, we used logistic regression (Agresti, 1996) to assess whether there was a positive correlation between occupancy rate and the probability that $\lambda_{pf} = 1$. Therefore, we performed what is analogous to a one-tailed test with the null hypothesis that occupancy rate and λ_{pf} of territories were correlated using an information-theoretic approach (see below). We used the G^2 goodness-of-fit test and the Pearson statistic (Agresti, 1996) to assess whether the data fit a logistic distribution. We adjusted variances and covariances for overdispersion from a binary distribution by using an overdispersion parameter (Burnham and Anderson, 1998).

We created two models to investigate whether there was a correlation between λ_{pf} and occupancy. First, we calculated parameter estimates from a means (intercept only) model [expressed as $\text{logit}(P_{\lambda_{pf}=1}) = \beta_0$, where $P_{\lambda_{pf}=1}$ is the probability that $\lambda_{pf} = 1$]. Then we calculated parameter estimates from a model containing occupancy rates as a predictor variable [expressed as $\text{logit}(P_{\lambda_{pf}=1}) = \beta_0 + \beta_1(\text{occupancy rate})$]. We then estimated quasi-likelihood estimates of $QAIC_c$ (Burnham and Anderson, 1998) to rank the two models because we included an overdispersion parameter when comparing models. If the model containing occupancy was ranked higher (lower value of $QAIC_c$) than the means model, we concluded that the slope parameter for occupancy was not equal to zero and that occupancy positively correlated with the probability that $\lambda_{pf} = 1$ (i.e., sites where females were more likely to replace themselves). The sign of the estimate indicated whether the correlation was positive or negative. Further, we used a 95%

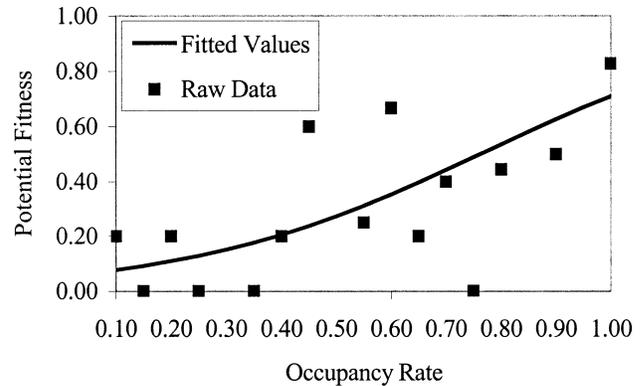


Figure 2

Comparison of raw data (grouped into bins of 5% occupancy rate) to fitted values illustrating variation between occupancy rates and territory fitness potential in the San Bernardino Mountains, California, from 1989 to 1998.

likelihood ratio confidence interval of the estimate to assess the strength of evidence that a parameter estimate was different from zero. Confidence intervals that did not include zero provided strong evidence that a parameter estimate was different from zero. Logistic regression analyses were done using SAS software (Proc GENMOD; SAS Institute, 2000).

RESULTS

We identified and monitored 142 spotted owl territories between 1989 and 1998. We eliminated 14 territories from the analysis because of missing data. The overall occupancy rate of territories declined from 89% in 1989 to approximately 50% in 1998, but the trend was not constant over time. Occupancy rate decreased between 1989 and 1992, remained stable until 1996, then declined to 50% by 1998 (Figure 1). Occupancy rates within territories ranged from 10% to 100%. Annual apparent survival estimates averaged across years, and individuals on each territory ranged from 0 to 1. Although reproductive output was high for some individuals over the course of their lives (maximum = 16), these values were halved (to adjust reproductive output so that it represented fecundity) and averaged across years for each territory, resulting in annual fecundity estimates that ranged from 0 to 1. Standard errors of apparent survival estimates ranged from 0.00 (territories where the same owls were observed on the site throughout the study period) to 0.36. Standard errors of fecundity ranged from 0.25 to 0.78.

All three estimates of model fit indicated that the data fit a logistic distribution (G^2 goodness-of-fit test: $P = 0.09$; Pearson statistic: $P = 0.42$; overdispersion parameter = 1.18). The model that included occupancy was ranked substantially higher ($QAIC_c = 95.43$) than the means model ($QAIC_c = 151.41$). The parameter estimate for occupancy (estimate = 3.74, 95% likelihood ratio confidence interval = 1.98, 5.78) indicated that the correlation was positive, adding additional support that occupancy correlated with λ_{pf} (Figure 2). Thus, spotted owls in our study tended to occupy sites where they were more likely to at least replace themselves during this study. Although occupancy generally correlated with λ_{pf} in this study, we detected considerable scatter from a smooth relationship (Figure 2).

DISCUSSION

Many previous studies of spotted owl population dynamics have estimated temporal variation in survival and fecundity to

describe variability in these parameters (e.g., Franklin et al., 2000; Seamans et al., 1999). These authors were interested in estimates of temporal variation for their respective populations, whereas we investigated spatial variation in survival and fecundity within our study population. We suspected that the high spatial variation in survival and fecundity in our study resulted from a combination of habitat (Franklin et al., 2000; Gutiérrez et al., 1992), social factors (Forsman et al., 1984; LaHaye et al., 2001), individual characteristics of resident owls (Łomnicki, 1988), and stochastic differences among territories. However, additional data collection and analyses would be necessary to explain trends in spatial variation of demographic parameters in this population.

The IFD model (Fretwell and Lucas, 1969) was one of the first mechanisms proposed to conceptualize spatial distribution and settlement patterns in animals within their preferred habitat. The territorial behavior of spotted owls (Gutiérrez et al., 1995) led us to predict that they would follow an IDD rather than an IFD because dominant individuals should gain access to higher quality territories. Ens et al. (1995) described six criteria that needed to be met under an IDD. We did not have data to test four of the six criteria. However, we explored differences in fitness potential among territories and whether competitors occupied territories with the highest fitness potential.

Franklin et al. (2000) investigated whether spotted owls in their study area followed an IDD or IFD by calculating habitat fitness potential values for each territory. Specifically, they used habitat covariates to model survival and fecundity of individual owls. The regression equation developed from their modeling was then used to back-transform to territory-specific estimates of survival and fecundity. These estimates represented values that would be expected of an individual owl if it settled in a territory based on the habitat characteristics of that territory. These back-transformed survival and fecundity estimates were then incorporated into a single estimate of habitat fitness potential for each territory. Because Franklin et al. (2000) documented spatial process variation among habitat fitness potential estimates of territories, they predicted that owls in their study area followed an IDD. We did not use habitat in our estimates of fitness potential because preliminary modeling indicated that habitat was not correlated with survival and fecundity in our study area (LaHaye, unpublished data). Nevertheless, we also observed spatial variation in overall fitness potential estimates among territories. In addition, spotted owls in the San Bernardino Mountains appeared to recognize site-quality differences among territories because occupancy rates correlated with estimates of λ_{pf} .

Although occupancy correlates with our binary, categorical measure of λ_{pf} (higher fitness, lower fitness), our data indicate that there is still considerable variation in the relationship. This variation may be due to (1) an inherent inability to rate territory quality (Levin et al., 2000), (2) the inability of some owls to correctly assess site quality because large home range sizes limit the number of territories an individual can sample (Pulliam and Danielson, 1991), (3) inability of individuals to predict high-quality sites when resources are temporally variable, (4) high costs of movement (Kennedy and Gray, 1997; Levin et al., 2000), (5) population status relative to carrying capacity (i.e., a declining population versus an increasing population; Bautista et al., 1995), (6) competition (Spencer et al., 1995), (7) individual differences in ability to secure resources that are present (Spencer et al., 1995), and (8) dispersal processes (e.g., the need to secure a mate; LaHaye et al., 2001). In addition, the low precision of our territory-specific demographic estimates could introduce considerable variation from a smooth relationship between

occupancy and fitness in this analysis due to high standard errors in λ_{pf} estimates and associated difficulties in converting values near 1 to a binary response variable. Further, our inability to include individual covariates (e.g., age of territorial owls) implies that individual characteristics of owls on territories are confounded with λ_{pf} estimates.

Densities of woodrats, the main prey species in our study area (Smith et al., 1999), are temporally and spatially dynamic (Ward et al., 1998; Williams et al., 1992), which may complicate settlement decisions. In addition, dispersing owls may discern high-quality sites from those that can be occupied, but are of low quality, partially by the presence of conspecifics (LaHaye et al., 2001; Stamps, 1988). However, site selection based on conspecifics assumes birds already occupying territories are in the highest quality sites. Further, large territories may be difficult to assess by dispersing spotted owls. For example, Pulliam and Danielson (1991) argued that spotted owls should not conform to ideal selection because their home ranges are large and dispersal mortality is high, which reduces the number of breeding sites that a dispersing owl can sample. In addition, once an owl settles in a territory that provides enough resources to survive and reproduce, it may not be adaptive to move and gamble that it would find both a better territory and a mate (Levin et al., 2000). Hirons (1985) suggested that tawny owls (*S. aluco*), and perhaps other owls, must learn the best hunting sites in a territory to successfully breed. Accumulating such knowledge about the territory in a short time period would be nearly impossible for spotted owls because they have large home ranges (Gutiérrez et al., 1995). Thus, the cost of abandoning a territory in which an owl has invested significant exploration time would need to be balanced against the risks of moving to a territory of equal or lower quality. It may not be worth risking the loss of accumulated knowledge of a territory, even if it is not the best territory, given the longevity of spotted owls. For example, some owls may live long enough to contribute to the next generation even when occupying a lower quality territory simply because they could experience a range of prey densities during their lifetime, allowing them to reproduce at irregular intervals. In summary, we suspect that the variability in our data largely resulted from a combination of the ecological factors discussed and the low precision of our demographic estimates.

Our results support conclusions from previous work suggesting that wild populations of spotted owls appear to follow IDD rather than an IFD (Franklin et al., 2000). In addition, we add additional support for the IDD by addressing a second assumption: that spotted owls can recognize and do occupy high-quality sites. However, we found an imperfect fit between occupancy and λ_{pf} when we used a binary response variable as a measure of territory quality. This relationship may have been even weaker if the response variable was continuous. This led us to explore potential causes for the deviation from ideal selection in this analysis. It may be unreasonable to expect ideal site selection at the scale of owl home ranges (Pulliam and Danielson, 1991), especially if this assessment is influenced by an imperfect ability to rate the quality of sites, social stimuli for settling, the need to acquire a mate, and stochastic opportunities associated with site and mate availability in a natural population.

Because spotted owls may not always occupy sites with the highest potential fitness, demographic rates may be lower than expected in areas that have limited amounts of suitable owl habitat. This suggests that either reserve size for spotted owl conservation or amount of suitable habitat needed to maintain a viable population of spotted owls may be larger than predicted by vital rates alone due to factors that influence territory selection (Greene and Stamps, 2001).

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