

# Population models for social species: lessons learned from models of Red-cockaded Woodpeckers (*Picoides borealis*)

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**Abstract.** Behavior can have major impacts on the population dynamics of social species and should be incorporated into demographic models to realistically evaluate population trends and extinction risk. We compared the predictions of a stage- and age-based matrix model, an individual-based model (IBM, developed in the program Vortex), and a spatially explicit individual-based model (SEPM) with the actual dynamics of a population of Red-cockaded Woodpeckers (RCW; *Picoides borealis*) in the Sandhills of North Carolina, USA. Predictions, including population size, composition, and growth rate, differed the most from actual population characteristics for models that did not incorporate social structure. The SEPM most closely predicted actual population dynamics, underestimating the population by 2.3%. This model, specifically developed to simulate RCW population dynamics, contains many of the features that we assert are important for adequately incorporating social behavior into demographic and population modeling. These features include the ability to (1) differentiate individuals based on their stage class, (2) capture the dynamics of the population at both the individual and group level, (3) incorporate the positive or negative effects of subdominants, (4) include environmental and demographic stochasticity, and (5) capture dispersal and other spatial factors. The RCW SEPM, although currently species-specific, provides a strong blueprint for how population models for social species could be constructed in the future when data allow.

**Key words:** cooperative breeding; demographic models; matrix models; population models; population viability analysis; Red-cockaded Woodpeckers; sociality; Vortex.

## INTRODUCTION

Because endangered species are often not amenable to experimental manipulation, demographic modeling, including population viability analysis (PVA), is a powerful tool for recovery planning. Such models offer the rigorous use of quantitative methods to establish population trends and to forecast the future status and extinction risk of populations in the face of both anthropogenic threats and stochastic processes (Frankham et al. 2002, Morris and Doak 2002) while also enabling the user to evaluate the efficacy of management scenarios (Beissinger and Westphal 1998). Like any model, demographic models are rarely intended to be more than simplified representations of real systems, and it is recommended that models be as simple as possible to be parsimonious while reflecting the limitations of data and knowledge (Noss et al. 1997, Ralls and Taylor 1997, Ruckelshaus et al. 1997, Beissinger and Westphal 1998, Groom and Pascual 1998). However, to adequately predict population trends and to be useful tools for endangered species recovery planning, demographic models must still be complex enough to capture critical

components of the focal system (Letcher et al. 1998, Stephens et al. 2002).

Social behavior, for example, is one such critical element that should be included in models of species with strict social structures because this behavior can affect survival, reproduction, and other population dynamics.

In some ecological systems, social behavior can increase a species' risk of extinction through a variety of mechanisms. For instance, social behavior often leads to the reproductive suppression of subordinate group members and restricts the number of breeders in a population to the number of social groups, making small populations more vulnerable to risks related to demographic stochasticity and habitat fragmentation (Vucetich et al. 1997, Walters et al. 2002a). Studies have demonstrated that extinction risk for social species like gray wolves (*Canis lupis*), African wild dogs (*Lycaon pictus*), and Red-cockaded Woodpeckers (RCWs; *Picoides borealis*; see Plate 1) is strongly correlated with the number of social groups in the population (Vucetich et al. 1997, Walters et al. 2002a, Somers et al. 2008) and not necessarily the number of individuals.

In addition, social groups may depend on a critical number of non-breeding group members for foraging, predator defense, or successful reproduction (Allee et al. 1949). For example, the vigilance system utilized by dwarf mongoose (*Helogale parvula*) becomes less effec-

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tive when the group size is smaller than five individuals, and mortality is significantly higher for individuals in small groups (Rasa 1989). Similarly, White-winged Choughs (*Corcorax melanorhamphos*) and Striped-back Wrens (*Campylorhynchus nuchalis*) rarely breed successfully when a group is smaller than four individuals (Rabenold 1984, Heinsohn 1992). As a result, social species may be particularly vulnerable to stochastic events that depress group size below thresholds necessary for critical social functions, which can quickly lead to the loss of the entire group (Courchamp et al. 1999).

Social behavior can also lead to the aggregation of individuals, increasing the probability of extinction following a single catastrophic event, such as a fire or disease epidemic, for species with only a small number of individuals or populations remaining (Reed 1999). Finally, social behavior, which typically limits breeding opportunities to a few dominant territory holders, can lead to aggressive competition for territories, ultimately resulting in delayed reproduction, decreased territorial productivity, and decreased speed in population recovery (Lopez-Sepulchre et al. 2009). For instance, social structure leads to reproductive suppression and social conflict in Seychelles Magpie Robins (*Copsychus sechellarum*); less experienced subdominants often aggressively take breeding opportunities from experienced breeders, leading to longer intervals between fledglings and lower productivity in the territory (Lopez-Sepulchre et al. 2009).

In other ecological systems, social behavior can have positive influences and reduce extinction risk. Helper activities (e.g., bringing food to the breeding pair) can protect breeders during times of environmental stress, ultimately increasing reproductive success (Heppell et al. 1994) and survival (Grimm et al. 2003, 2005) and thus reducing environmental stochasticity. For example, in alpine marmots (*Marmota marmot*), the presence of even a single subdominant individual in a breeding territory boosts the survival of the breeding pair by 30%, and the presence of two subdominants boosts survival by as much as 50% during winter months (Grimm et al. 2003). For RCWs, significantly more fledglings are produced in groups that contain at least one helper, and fledgling success increases with the number of helpers (Heppell et al. 1994, Conner et al. 2004). In addition, helpers reduce the amount of variability in reproductive success (Reed and Walters 1996) and increase breeder survival rates (Khan and Walters 2002), both of which increase fitness in RCWs.

Furthermore, the broader class of helpers and floaters (i.e., individuals that have dispersed from their natal territories but have yet to find a new territory or group to join) provides a population buffer as these individuals take over breeding vacancies as they arise (Heppell et al. 1994, Letcher et al. 1998, Walters et al. 2002a, Grimm et al. 2005). Thus, the critical breeding population often stays the same as the larger population fluctuates,

reducing the population-level impacts of environmental stochasticity (Letcher et al. 1998, Grimm et al. 2005).

Despite the fact that social behavior can have major impacts on population dynamics, it is rarely considered in models of extinction risk (Reed 1999), likely due to a lack of existing modeling platforms that can easily incorporate this behavior. The RCW is one of a few examples of a cooperatively breeding social species for which a demographic model that incorporates social behavior exists (but see models for the Florida Scrub Jay, *Aphelocoma coerulescens* [Stith et al. 1996]). Our objective in this study was to examine RCW models that vary in complexity and in their consideration of social structure to determine how the predictions of these models differ from each other and from observed population trends. It was also our intention to highlight lessons learned as RCW models were developed from simple stage-based Lefkovich matrices to complex spatially explicit individual-based models in order to guide continued model development for other social species.

## METHODS

### *Study system*

The RCW is an endangered species endemic to fire dependent longleaf pine ecosystems in the southeastern United States. Primary threats to the species include a lack of suitable cavity trees, habitat fragmentation (Conner and Rudolph 1991), and fire suppression that results in hardwood midstory encroachment and the declining suitability of foraging habitat (James et al. 2001, Walters et al. 2002b).

Preferred habitat for the species consists of mature, open pine forest with large trees, sparse midstory, and a lush herbaceous ground cover (Hardesty et al. 1997, James et al. 2001, Walters et al. 2002b, U.S. Fish and Wildlife Service 2003), conditions primarily maintained through frequent, low-intensity ground fires (Frost 1998). Old pines are an especially important part of RCW ecology because RCWs construct cavities in living trees, and heartwood diameter is a function of age. Cavity construction is difficult and time intensive (Harding and Walters 2004), and RCW groups will defend and use the same cavity trees for many years. Consequently, cavity trees within RCW territories largely determine the distribution and number of individuals/groups in an area (Ligon 1970, Walters et al. 1992), and population dynamics often revolve around existing territories and the clusters of cavity trees within them (Walters 1991).

RCWs are territorial and cooperatively breeding with a complex social structure. Most groups consist of two to four birds (range: one to seven birds; Walters 1990) that defend territories ranging from 71–152 ha (Conner et al. 2001). Groups are composed of a monogamous breeding pair and non-breeding helpers, which are typically male offspring of the male breeder (Walters 1990). Fledglings either remain on the natal territory as

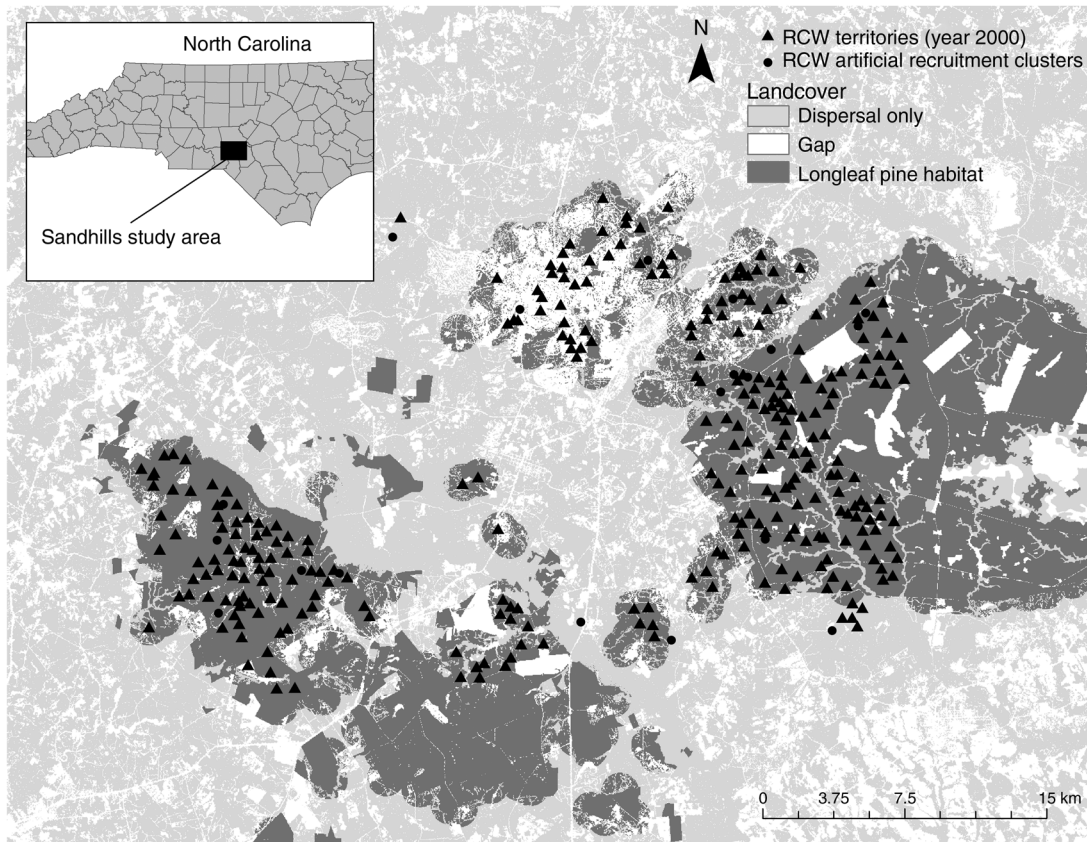


FIG. 1. The Red-cockaded Woodpecker (RCW) population in the Sandhills region of North Carolina, USA, from 2000 to 2010. The RCW territory layer and the Sandhills landcover layer shown here were the main inputs used in the spatially explicit RCW population model (i.e., the RCW SEPM).

helpers or disperse. Almost all females disperse in either the fall or spring following fledging and ultimately obtain breeding positions if they survive, although they may act as floaters before acquiring a breeding opportunity. Substantial numbers of male fledglings stay as helpers, and those that survive ultimately inherit the breeding position in their natal territory or fill breeding vacancies in neighboring territories. Other male fledglings disperse to either become breeders, solitary males, floaters, or (to a lesser extent) helpers in another territory. Male breeders are highly site faithful, although solitary males are more likely to abandon their territories (Walters 1990).

The presence of helpers and floaters is critical to the population dynamics of RCWs. Helpers participate in territorial defense, construction and maintenance of nest cavities, incubation, and care of nestlings and fledglings (Lennartz and Harlow 1979), which improve the reproductive success of the breeding pair (Heppell et al. 1994). In addition, because helpers and floaters take over breeding vacancies, these individuals provide a buffer that can reduce the negative impacts of environmental stochasticity (Heppell et al. 1994, Walters et al. 2002a). However, these benefits are only realized when

groups are sufficiently close and habitat fragmentation is low so that helpers, floaters, and dispersers can reach breeding vacancies (Walters et al. 2002a). For these reasons, we believe that incorporating both social structure and spatial factors should be critical in accurately modeling RCW population dynamics and those of other species with similar characteristics (Letcher et al. 1998, Courchamp et al. 1999, Walters et al. 2002a, Grimm et al. 2003, 2005).

#### Model parameterization

We calculated demographic rates from a long-term RCW data set for the Sandhills region of south-central North Carolina, USA (J. R. Walters, *unpublished data*; Fig. 1) that included the number of deaths, births, reproductive females, and stage-class transitions within the population on an annual basis (see Walters et al. [1988a] for details of data collection). We focused our analysis on RCW demography from 2000 to 2010 for the 5309 different birds that were banded in the population during that time.

Banded individuals were classified according to age and stage class each year, with potential stage classes including fledglings, individuals <1 year old; breeders,

TABLE 1. Sex-, stage-, and age-based Red-cockaded Woodpecker life history parameters used in population models (with the exception of the spatially explicit model, which was parameterized with observations of the species in the Sandhills region from 1980–1994).

Stage/Age	Annual survival	Annual transition probability to				Annual fecundity
		Breeder	Helper	Solitary	Floater	
<b>Male</b>						
Fledgling	0.479 (0.060)	0.042	0.373	0.016	0.047	0.04
Breeder	0.781 (0.044)	0.768	0.001	0.009	0.003	0.84
Helper	0.779 (0.035)	0.210	0.547	0.011	0.011	0.23
Solitary	0.779 (0.088)	0.550	0	0.214	0.015	0.60
Floater	0.599 (0)	0.401	0.050	0.044	0.104	0.43
Year 0–1	0.479 (0.060)					0.30
Year ≥1	0.773 (0.043)					0.48
<b>Female</b>						
Fledgling	0.333 (0.038)	0.222	0.047		0.063	0.24
Breeder	0.713 (0.041)	0.703	0.001		0.008	0.76
Helper	0.587 (0.032)	0.349	0.214		0.024	0.38
Floater	0.647 (0)	0.476	0.054		0.118	0.52
Year 0–1	0.333 (0.038)					0.24
Year ≥1	0.704 (0.040)					0.50

*Notes:* For annual survival, the SD due to environmental stochasticity is shown in parentheses. A value of 0 indicates that all variation in that parameter was due to demographic stochasticity for the study period. Fecundity was based on a post-reproductive census and is defined as the number of sons (or daughters) born per breeding male (or female) per year.

males and females that occupy a territory and have the potential to produce offspring; helpers, nonbreeding adults that are part of the social group and assist breeders; solitary males, adult males that maintain a territory but are unpaired and do not breed; and floaters, adults without territories that do not breed (Walters 1990). From this information, we calculated age- and stage-based average mortality, clutch size, percentage of females breeding, percentage of males breeding, and stage transition rates (Table 1). We also determined annual variation in these rates due to environmental stochasticity according to Akçakaya (2002; Table 1). The age-based demographic rates were subsequently used to parameterize the Leslie matrix and the individual-based model (IBM), while the stage-based demographic rates were used to parameterize the Lefkovich matrix and the individual-based spatially explicit population model (SEPM). Data used for the parameterization and validation of the matrix models and the IBM were not independent, but data used to parameterize the SEPM were based on previous observations of RCWs and were independent of data used for validation purposes. However, we do not believe that this influenced results because we examined peak model performance and primarily compared models against each other, and this difference was conservative with respect to the better performance of the most complex model.

#### *Population models*

One objective of our study was to compare the results of demographic models with varying abilities for incorporating complex social structure. We specifically compared the annual population size and the stage or age composition predicted by a stage-based Lefkovich

matrix, an age-based Leslie matrix, an IBM, and an SEPM with the actual observed dynamics of the Sandhills RCW population. These specific model types and programs were chosen because they have been used to model RCW dynamics previously and, with the exception of the SEPM, have been used extensively for a wide variety of species including those that exhibit social dynamics.

*Lefkovich and Leslie matrices.*—The simplest models explored in this study were male-only, matrix models based on either age (Leslie matrix) or stage class (Lefkovich matrix). Both types of matrices were deterministic, and the stage-based Lefkovich matrix incorporated a rudimentary degree of sociality in the population model that the Leslie matrix did not. A Lefkovich matrix was used previously to evaluate management scenarios for RCWs in the North Carolina Sandhills (Heppell et al. 1994). As in Heppell et al. (1994), matrices were constructed in this study as male-only models because, unlike females, males almost exclusively comprise the helper class and can hold territories despite being unpaired. Thus, male dynamics better reflect overall population dynamics. For both the Leslie and Lefkovich matrices, elements in the body of the matrix reflected the probability that an individual will survive and progress to the next age or stage, with values in the matrix's top row representing age- or stage-based fecundity (Caswell 2001). We calculated fecundity as the number of male fledglings produced by individuals that survived the year and became adult breeders within the census period (i.e., a post-reproductive census model). For more information on the general structure of the Leslie and Lefkovich matrices, please see Caswell (2001) and Appendix A.

*Individual-based model.*—Next, we explored RCW population dynamics predicted by an IBM in the open platform Vortex, version 9.99 (Appendix B; Lacy et al. 2010). Vortex is a widely used, previously validated (Brook et al. 2000) program for PVA that simulates the effects of both deterministic forces and demographic, environmental, and genetic stochastic events to assess extinction risk. A similar Vortex model was used previously to assess the viability of RCWs at the Savannah River site by Haig et al. (1993).

In this program, we created a two-sex model parameterized according to the age-based reproduction and mortality rates specific to the Sandhills RCW population (also used in the Leslie matrix; Table 1). This model was stochastic and did not incorporate sociality. We assumed that RCWs could breed between the ages of 1 and 14 years and that reproduction occurred in monogamous pairings that could result in a maximum of five offspring per year. Because of the social structure exhibited in RCW populations, we also assumed that only a fraction of adult males (56.6%) and females (66.4%) could breed in a given year (calculated as the number of adults  $\geq 1$  year old that produced offspring out of the total number of adults; J. R. Walters, *unpublished data*). Environmental and demographic stochasticity were incorporated through probabilities of survival and reproduction. Although Vortex is capable of incorporating density dependence, inbreeding depression, and catastrophes, we did not include these parameters in order to better compare simulation predictions with other models used in this study.

*RCW-specific spatially explicit population model.*—The final and most complex model used was a two-sex, individual-based, SEPM created explicitly for RCWs (Appendix C; Walters et al. 2011) that runs as an add-on in ArcGIS version 10 (ESRI, Redlands, California, USA). This model, which was created to inform critical management decisions for RCW populations on military installations in the southeastern United States (Walters et al. 2011), is stochastic and incorporates a high degree of sociality into model simulations.

In general, simulations developed in the RCW SEPM are constructed as scenarios in ArcGIS with spatial layers for RCW cavity tree clusters (i.e., territories) and for the underlying landscape (Fig. 1). The map of cavity tree clusters, which shows all occupied and unoccupied territory centers at the start of a simulation, was created using  $x,y$ -coordinate data of known RCW territories in the Sandhills in the year 2000. We assumed that all territories were occupied at the start of the simulation, with the RCW population model randomly choosing group composition. This model also allows for the creation of new territories through budding (i.e., a process in which a single group splits into two when enough suitable habitat is available) or through the addition of sets of human-created artificial cavities, known as recruitment clusters. Because recruitment clusters were constructed in the Sandhills between 2000

and 2010, we added points for these additional cavity tree clusters throughout the course of simulations using the recruitment cluster option available within the program. Nineteen recruitment clusters were added to simulations in the model year associated with the actual year they were excavated in the field (Fig. 1). Two additional cavity clusters were naturally created by RCWs in the Sandhills between 2000 and 2010 through budding; we allowed budding to occur during simulations when an adequate amount of habitat was available (minimum 120 acres [1 acre = 0.405 ha]) to capture this process. However, the actual number and location of new, budded clusters cannot be controlled by the user in the RCW SEPM, and we did not specifically add these two budded clusters during the simulation. Although analogous processes were not included in the Leslie, Lefkovitch, or IBM, this should not lessen the value of the model comparison because reproduction was not constrained to territories in the nonspatial models.

The second spatial layer required to initiate any RCW SEPM simulation is the landscape layer, which provides a spatially explicit representation of the space available to the species for foraging, breeding, and movement. The landscape was divided into seven categories that delineated how that parcel could be used within the model: (1) pine, suitable for both breeding and foraging; (2–4) open, water, or other (all considered gaps), suitable only for the movement of some RCW classes; and (5–7) hardwood, low-suitability pine, or mixed pine–hardwood stands, suitable only for the movement of RCWs. We used a landscape layer of the Sandhills study region depicting these landcover classifications in the year 2000 previously created elsewhere (Walters et al. 2011).

During the course of any simulation within the RCW SEPM, individual RCWs are categorized based on a defined set of life history stage classes, which subsequently determine movement, mortality, and fecundity rates. At birth, males are added as fledglings that either (1) die within their first year, (2) remain in their natal territories as helpers, breeders, or solitary males or (3) disperse from their natal territories during their first year. Individuals that disperse either fill a breeding vacancy or become a solitary male or floater. Female fledglings exercise options 1 or 3. Dispersal range and landcover types over which individuals will travel are dependent on the sex and stage of the individual.

The user chooses stage-specific transition, mortality, and fecundity rates by selecting one of two demographic sub-models within the RCW SEPM. The Sandhills sub-model is based on observations of RCW populations in the Sandhills from 1980 to 1994 (Walters et al. 1988b, Letcher et al. 1998) while the Coastal sub-model is based on observations on Marine Corps Base Camp Lejeune in coastal North Carolina from 1986 to 2001 (Walters 2004). We selected the Sandhills sub-model for this study (Appendix C; see Letcher et al. [1998] for a detailed description of how these values are used to

TABLE 2. Observed Red-cockaded Woodpecker population size and structure between the years 2000 and 2010 in the Sandhills region of North Carolina, USA (J. R. Walters, *unpublished data*).

Year	Total population size				Males					Females			
	All	All adults	Males	Females	Fledgling	Breeder	Helper	Solitary	Floater	Fledgling	Breeder	Helper	Floater
2000	987	593	564	423	195	215	131	15	8	199	209	5	10
2001	894	610	522	372	139	219	137	16	11	145	215	6	6
2002	1030	644	592	438	191	231	143	14	13	195	226	6	11
2003	949	654	562	387	158	230	134	15	25	137	222	5	23
2004	1055	682	610	445	191	236	150	15	18	182	233	13	17
2005	113	775	646	467	162	255	196	13	20	176	251	19	21
2006	1254	772	728	526	247	261	192	12	16	235	258	11	22
2007	1263	837	723	540	214	266	202	14	27	212	264	26	38
2008	1181	768	667	514	204	270	168	9	16	209	265	18	22
2009	1255	778	701	554	241	270	154	8	28	236	267	17	34
2010	1238	736	682	556	238	266	153	10	15	264	262	16	14

determine demographic rates). Thus, demographic rates used in our specific scenario within the RCW SEPM were not those observed in the Sandhills population from 2000 to 2010 as shown in Table 1 or those used in the matrices and IBM, but they do serve as a close approximation for comparison purposes. Demographic and environmental stochasticity were also incorporated into the RCW SEPM's survival and fecundity rates (see Letcher et al. 1998, Walters et al. 2002a).

#### *Simulations and validation*

To the degree possible, we initialized each model with the population size and structure recorded in the Sandhills region in the year 2000 (Table 2; J. R. Walters, *unpublished data*). We initialized the male-only Leslie and Lefkovich matrices with a population size and composition identical to those of the actual Sandhills population in 2000 (Table 2); models were initialized with 564 male individuals, 369 of which were adults. These matrices were then projected 10 years using the Microsoft Excel (Redmond, Washington, USA) add-in PopTools version 3.2.5 (Hood 2010) to determine the predicted population size and structure each year up to the year 2010. Because Vortex considers both sexes and does not include the number of individuals in the 0–1 age class in a population census, we initialized the model with 593 individuals, reflecting the number of males and females age 1 year and older that were observed in the Sandhills population in the year 2000. The exact number of individuals of each age was unclear from population observations, so we used the default stable age distribution automatically generated in Vortex (which calculates the equilibrium stable age distribution as a function of population size, reproductive rates, and survival rates input by the user). Thus, population composition may not have precisely reflected the actual age-specific composition observed in 2000. The RCW SEPM, although an individual-based model, was initialized using a map of territory locations and not with population abundance. The program calculates the number and stage distribution of individuals in the population based on the user-specified number of

occupied territory locations, average group size, and demographic module. We initialized the model under the Sandhills sub-model, which assumes that 10% of occupied territories contain a solitary male and that the remaining 90% of territories contain a breeding pair (with 50% of those 90% also containing helpers). With an average group size of 2.65 individuals and 233 occupied territories, our model was initialized in the year 2000 with 617 adult individuals, which overestimated population size compared to the 593 adults actually observed in the Sandhills population in 2000. Population stage distribution also may not exactly match the actual stage distribution observed in 2000, but Letcher et al. (1998) determined that the results of the RCW SEPM were not sensitive to the initial stage distribution of individuals. Both Vortex and the SEPM were simulated at an annual time step for 10 years with 70 stochastic iterations per simulation year.

We compared the results of the four models to the size of the actual Sandhills RCW population each year up to the year 2010 (Table 2; J. R. Walters, *unpublished data*). We further extrapolated model results in some instances to correct for inconsistencies in model outputs. For example, both Vortex and the SEPM consider only adults in their calculations of population size, the matrix models output only the number of male RCWs in each age- or stage class, and the RCW SEPM does not separate population size estimates by sex. Therefore, in order to compare all models, we extrapolated the estimated two-sex population size for the matrix models by multiplying the total predicted number of adult males by 0.37 (given that the male : female sex ratio was 0.63 in the Sandhills between 2000 and 2010; J. R. Walters, *unpublished data*) and adding this number to the total number of adult males. Using this extrapolation, we were able to compare the predicted number of adults between models as well as between predicted and observed totals.

## RESULTS

In the Sandhills region of North Carolina, the observed RCW population increased from 593 adults

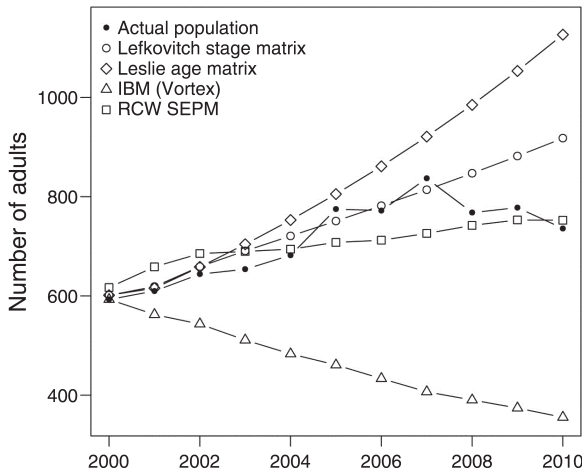


FIG. 2. The number of adults predicted each year from 2000 to 2010 by the four demographic models used in this study compared to the actual population size (solid symbols) for RCW in the Sandhills region of North Carolina. In order to overcome inconsistencies in model outputs for comparison between models, we extrapolated the total estimated population size from the number of males predicted by the Leslie and Lefkovitch matrices, assuming an adult female to adult male sex ratio of 0.63 (as seen in the Sandhills population between 2000 and 2010 [J. R. Walters, unpublished data]). Models compared included a male-only age-based Leslie matrix (non-social, deterministic), a male-only stage-based Lefkovitch matrix (social, deterministic), a two-sex individual-based model (IBM) developed in the program Vortex (non-social, stochastic), and a two-sex spatially explicit individual-based model developed specifically for RCWs (RCW SEPM; social, stochastic).

in 2000 to 736 adults in 2010 (finite rate of population increase,  $\lambda = 1.02$ ). Of the four simulation models, the age-based models predicted population trends that most differed from the actual population dynamics (Fig. 2): the Leslie matrix predicted an increase from 601 to 1127 adults; ( $\lambda = 1.06$ ), and the IBM (Vortex) predicted a decrease from 593 to 355 adults ( $\lambda = 0.94$ ). The Leslie matrix overestimated the predicted population size in 2010 by 53%, and the IBM underestimated the 2010 population size by 52%. Conversely, the stage-based models more closely predicted the actual population trends (Fig. 2). The Lefkovitch matrix predicted that the population would increase from 369 to 563 adult males (an estimated increase from 601 to 918 adults;  $\lambda = 1.04$ ) and overestimated the 2010 population by 25%. The RCW SEPM best predicted population size in the year 2010; the model predicted that the population would increase from 617 to 753 adults ( $\lambda = 1.01$ ) and underestimated the 2010 population by 2.3%.

#### DISCUSSION

Our results illustrate that the incorporation of social structure is important for simulating realistic population dynamics for social species; the two demographic models that included social structure (i.e., the Lefko-

vitch matrix and the RCW SEPM) best predicted the population size and composition of the observed RCW population in the Sandhills region of North Carolina. We also found that the RCW SEPM, which was the most complex model because it incorporated social structure in both vital rates and movement, most accurately predicted the size of the RCW population in 2010. These results support earlier recommendations that behavior is an important component that should be included in PVA and other population models used to determine extinction risk for endangered species (Reed 1999, Grimm et al. 2005).

The differences between models in their predictions of population size were striking, especially considering that demographic rates used to parameterize the models were based on observations of the same RCW population over the same time period. Comparisons of other population models have shown that multiple models can provide an equally good fit for data while yielding different predictions based on slight differences in input formats or computational routines (Werner and Caswell 1977, Mills et al. 1996, Pascual et al. 1997). Predictions likely differed in this study because of the inclusion (or omission) of female demographic rates, social structure, stochasticity, and spatial distribution, and whether a given model ultimately overestimated or underestimated the RCW population size (both compared to other models and compared to the actual RCW population) could be attributed to the balance of these combined factors (Table 3).

One major driver of the differences between model predictions involved how reproductive constraints were considered. In actual RCW populations, reproduction is limited to specific stage classes (i.e., breeders) and to territory clusters. Therefore, models that do not consider these constraints would be expected to overestimate reproduction and, consequently, population size. Models that lack territorial constraints on reproduction would especially overestimate reproduction (and population size) for fragmented populations where, in the actual population, unpaired adults are unable to reach breeding vacancies. This circumstance could only be accounted for in a spatially explicit model like the RCW SEPM.

Furthermore, models that consider the number of breeders only as a fraction of the total population to account for stage class constraints on reproduction would likely underestimate population size in declining populations. In the Leslie and Lefkovitch matrices and in the IBM Vortex, it is generally assumed that a fixed percentage of the population breeds each year irrespective of population size, and, as the population declines, the number of individuals that breed also declines. However, in a real population of a social species like the RCW, the number of breeders would actually remain stable even as the population declines (up to some threshold) if floaters and helpers are able to take over breeding vacancies. This issue was particularly magni-

TABLE 3. Parameters that may have caused an increase or decrease in model predictions compared to actual Red-cockaded Woodpecker (RCW) population trends and to the predictions of the other models tested.

Effect on population estimate	Age-based Leslie matrix (nonsocial, deterministic)	Stage-based Lefkovich matrix (social, deterministic)	Vortex (nonsocial, individual-based, stochastic)
Could inflate	<ol style="list-style-type: none"> <li>1) Did not include females (limiting sex).</li> <li>2) Reproduction not constrained to stage class.</li> <li>3) Reproduction not constrained to territory cluster (effect magnified in fragmented populations).</li> <li>4) Did not include environmental or demographic stochasticity.</li> </ol>	<ol style="list-style-type: none"> <li>1) Did not include females (limiting sex).</li> <li>2) Reproduction not constrained to territory cluster (effect magnified in fragmented populations).</li> <li>3) Did not include environmental or demographic stochasticity.</li> </ol>	<ol style="list-style-type: none"> <li>1) Reproduction not constrained to stage class.</li> <li>2) Reproduction not constrained to territory cluster (effect magnified in fragmented populations).</li> </ol>
Could inflate or deflate†	<ol style="list-style-type: none"> <li>1) Adult mortality averaged across all stage classes. Impact depends on population composition.</li> </ol>		<ol style="list-style-type: none"> <li>1) Adult mortality averaged across all stage classes. Impact depends on population composition.</li> </ol>
Could deflate	<ol style="list-style-type: none"> <li>1) Constrained reproduction to a percentage of adult population (important for declining populations).</li> <li>2) Did not consider stabilizing effect of social structure.</li> </ol>	<ol style="list-style-type: none"> <li>1) Constrained reproduction to a percentage of adult population (important for declining populations).</li> </ol>	<ol style="list-style-type: none"> <li>1) Constrained reproduction to a percentage of adult population (effect magnified if constrained by percentage of females; important for declining populations).</li> </ol>
Overall comparison	<p>Overestimated population size compared to other models.</p> <p>Overestimated population size compared to actual RCW population dynamics.</p>	<p>Overestimated population size compared to other models (except Leslie matrix).</p> <p>Overestimated population size compared to actual RCW population dynamics.</p>	<p>Underestimated population size compared to other models.</p> <p>Underestimated population size compared to actual RCW population dynamics.</p>

*Note:* Whether a model ultimately under- or overestimated RCW population size was the result of the balance in the effects of these parameters.

† Impact on model results dependent on the model scenario and initial population trend.

fied in Vortex because a percentage was used for the number of breeding females, which have higher mortality rates (further overestimated by averaging across stages; see next paragraph) and are the limiting sex. When Vortex was parameterized such that all adult females but only 56.6% of the males could breed (i.e., the percentage of males considered breeders in the actual population; J. R. Walters, *unpublished data*), predictions were identical to those of the Leslie matrix (results not shown). However, when all males could breed but only 66.4% of the females could breed (i.e., the percentage of females considered breeders in the actual population; J. R. Walters, *unpublished data*), the population rapidly declined (results not shown).

The inclusion (or omission) of stage-based mortality could have further impacted model predictions depending on the year or the distribution and composition of the population. For example, in the age-based models (i.e., the Leslie matrix and Vortex), mortality rates for adults were calculated as the average mortality for all individuals over the age of 1 year. However, in an actual RCW population, floaters have higher mortality rates compared to the other stage classes (Table 1). Thus, in the age-based models that do not differentiate mortality by stage class, mortality could be overestimated (if the

observed population had a large number of floaters) or underestimated (if the observed population had a small number of floaters) in calculations depending on the population composition, and this would translate into corresponding over- and underestimates in population size.

Finally, a model's treatment of environmental and demographic stochasticity could impact predictions of population size or extinction risk, particularly for small populations. Environmental and demographic stochasticity can decrease long-term population growth rates, and stochastic fluctuations in population size (related to either environmental or demographic stochasticity) can lead to chance extinctions (Lande 2002). As a result, models that do not incorporate environmental stochasticity (i.e., the Leslie and Lefkovich matrices) may overestimate population size (and underestimate extinction risk), particularly at small population sizes where subordinates are not available to reduce the impacts of environmental conditions on breeders. In addition, models that do not include social structure but do include stochasticity (i.e., Vortex) risk overestimating the impact of environmental stochasticity and underestimating population size by not considering the stabilizing effects of helpers and floaters. Furthermore, models





PLATE 1. Adult Red-cockaded Woodpecker. Photo credit: Michelle Juniso.

that do not consider demographic stochasticity or that do not consider the magnified effects of demographic stochasticity for species where reproduction is constrained to certain individuals or territories risk overestimating population size (and underestimating extinction vulnerability).

*Recommendations for models of social species*

These results underscore that, to accurately capture a social species' population dynamics, models should contain a number of specific features to address the impact that social structure can have on the population. The RCW SEPM contains many of these key model features and provides a blueprint for how models specific to other social species (or more generalized models capable of simulating any social species) could be developed in the future. These key features include (1) the ability to differentiate individuals based on sex, age, and/or stage class, given that survival and fecundity rates often differ as a function of these characteristics;

(2) the ability to capture dynamics at both the level of the individual and the territory/group, which allows the model to simulate population dynamics as a function of individual demography and the interactions among individuals within the confines of established groups; (3) the ability to incorporate the positive or negative effects of subordinates (or helpers), which can exacerbate the negative impacts of demographic stochasticity or minimize the effects of environmental stochasticity in many social systems; (4) the ability to incorporate stochasticity, particularly given that social structure can increase and decrease the negative effects of demographic and environmental stochasticity, respectively, in most social systems; and (5) the ability to capture spatial factors, which allows the model to consider the important effects of habitat fragmentation and territory distribution as individuals interact among the confines of established territories.

Finally, we acknowledge that, for many species, available data sets are not as extensive as that associated

with the RCW, and the model we advocate may appear to be far too complex for these lesser-studied systems. In these cases, the simple stage-structured Lefkovich matrix, which provided a relatively good estimate of population size, could provide a reasonable understanding of the system. The predictions of this type of matrix model could be further improved with added complexity, such as by considering multiple matrices that incorporate stochasticity into elements of survival and reproduction (Caswell 2001) or by including additional enhancements (Stott et al. 2012). However, if the effects of spatial structure, group size, and other aspects of the social system are strong enough, a more complex model, such as the one we employed, could provide more accurate predictions even in cases where all parameters are not known with certainty (Beissinger and Westphal 1998). In the case of social species, the trade-off between model complexity and the ability to estimate parameters may tilt more toward complexity than is typical.

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## SUPPLEMENTAL MATERIAL

## Ecological Archives

Appendices A–C are available online: <http://dx.doi.org/10.1890/13-1275.1.sm>