

# Florida Field Naturalist

PUBLISHED BY THE FLORIDA ORNITHOLOGICAL SOCIETY

---

VOL. 49, No. 3

SEPTEMBER 2021

PAGES 97-154

---

Florida Field Naturalist 49(3):97–109, 2021.

## VIABILITY OF A FLORIDA SCRUB-JAY (*Aphelocoma coerulescens*) POPULATION IN NORTH-CENTRAL FLORIDA

DUSTIN E. BREWER<sup>1</sup> AND RALPH RISCH<sup>2</sup>

<sup>1</sup>*Department of Biology, Institute for Great Lakes Research,  
Central Michigan University*

<sup>2</sup>*Florida Forest Service*

*Email: dustinbrewer92@yahoo.com*

**Abstract.**—Exceedingly limited breeding range, dispersal ability, and habitat connectivity tend to characterize species as at risk of extinction. A species endemic to Florida, the Florida Scrub-jay (*Aphelocoma coerulescens*; scrub-jay), exemplifies these characteristics, which have contributed to its alarming, roughly 90% population decline since the 1800s. To help stop or reverse this ongoing decline, land managers should communicate scrub-jay population trends to facilitate conversations about the effectiveness of respective management regimes within and between metapopulations and to identify regions in particular need of conservation focus. We report scrub-jay population survey data at Seminole State Forest (SSF) in north-central Florida between 2008 and 2016. Our data suggest a population high in 2008 ( $n = 137$ ), a low in 2015 ( $n = 90$ ), and 97 individuals in 2016. Using these data, we modeled a simple population viability analysis which can be easily replicated, and interpreted with caution, by those with similar count data. Our analysis indicated a 0.78 extirpation probability of scrub-jays at SSF within 100 years. Relatively small, simulated increases in population growth substantially decreased this probability. Given that SSF scrub-jays likely constitute the largest portion of their metapopulation, continued and perhaps increased support for management efforts at SSF may be required for metapopulation persistence. Our results highlight the importance of population monitoring with respect to validating current, and identifying the need for future, management efforts.

**Key words:** avian, corvid, population trends, Seminole State Forest, wildlife management

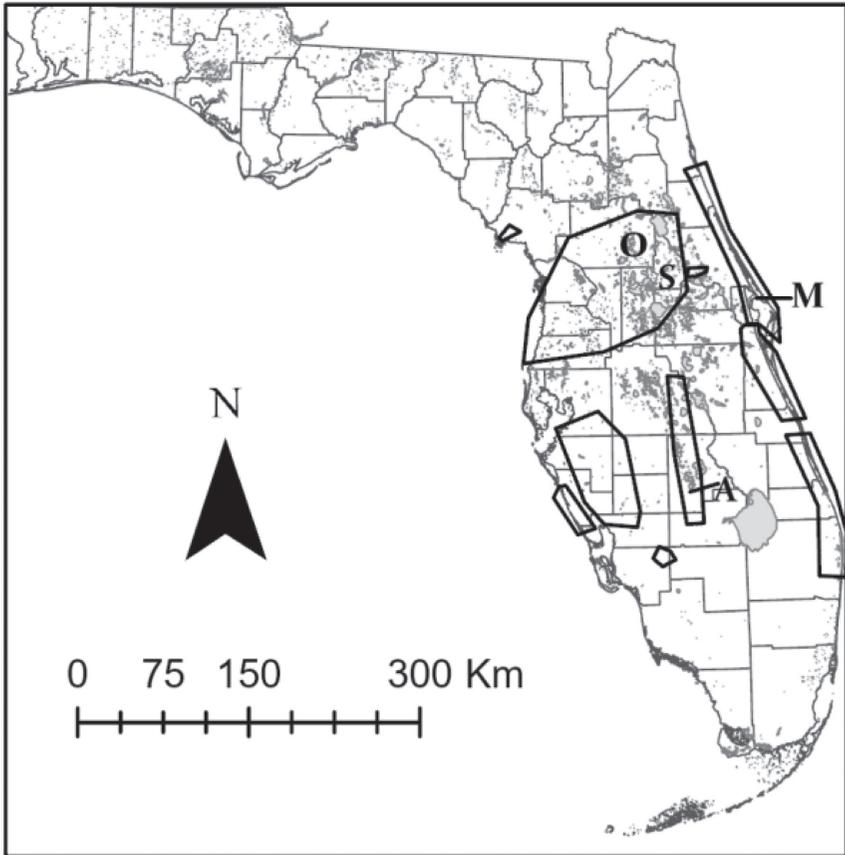
For species that are highly habitat-specialized, habitat loss is currently the most common ultimate cause of extinction (Fahrig 1997, Owens and Bennett 2000). Proximate causes for extinction other

than habitat loss include stochastic (random) processes regarding demography (e.g., births and deaths) and the environment (e.g., precipitation patterns, natural disasters; Simberloff 1995, Whitlock 2000). Species with a small population size, and especially those species that naturally inhabit small geographic ranges (i.e., range-restricted species), are particularly vulnerable to these proximate causes when suitable habitat area within those ranges has been substantially reduced (Harnik et al. 2012). Such habitat reduction can further isolate metapopulations (i.e., generally isolated groups of conspecific individuals between which dispersal occasionally occurs). For many extant species particularly vulnerable to these pressures, we do not know which metapopulations are viable (i.e., likely to persist 100 years into the future) because of a lack of monitoring. Metapopulations can be defined by the 99th percentile for the focal species' dispersal distance. Namely, all conspecific territories that can be linked together via straight lines less than that distance (one line between each adjacent territory) and that do not cross known hard barriers (like large water bodies) constitute a metapopulation (Stith et al. 1996).

The Florida Scrub-jay (*Aphelocoma coerulescens*; hereafter scrub-jay), endemic to Florida, exemplifies vulnerability and exposure to each of the above factors. Even before intensive anthropogenic land transformation began in the 1800s, scrub-jay metapopulations were relatively small, non-contiguous, and isolated because of extreme sedentariness (most scrub-jays disperse less than 3 territory widths [Woolfenden and Fitzpatrick 2020], a distance of ~1.2 km at SSF [D. E. Brewer, Central Michigan University, pers. obs.]) and dependence upon fire-mediated oak-scrub confined to sandy ridges, river corridors, and coasts. It has been estimated that the range-wide scrub-jay population has declined by more than 90% since the 1800s largely because of fire suppression and anthropogenic habitat conversion (Woolfenden and Fitzpatrick 2020). Though there have been extensive studies of scrub-jay biology at Archbold Biological Station (ABS; e.g., Woolfenden and Fitzpatrick 1984) and at or in the vicinity of Merritt Island National Wildlife Refuge (MINWR; e.g., Breininger et al. 2006), relatively few studies have occurred in other parts of Florida where at least 8 additional genetically distinct scrub-jay groups occur (Coulon et al. 2008). These 10 genetic groups, which likely reflect habitat connectivity prior to European settlement, contain metapopulations that have become increasingly isolated in the past 200 years because of anthropogenic habitat conversion (Coulon et al. 2008, Woolfenden and Fitzpatrick 2020). In the early 1990s, there were 42 extant scrub-jay metapopulations (each separated by >12 km; Stith et al. 1996) and a total population

size (~4,000 family groups) that was approximately 25% less than 10 years before (Woolfenden and Fitzpatrick 2020). Scrub-jay population declines have continued since the early 1990s in urbanizing areas (e.g., Miller and Stith 2002) and even on lands managed to sustain natural resources, including scrub-jays (Boughton and Bowman 2011). Many of the 42 metapopulations present in the early 1990s are now extirpated (Coulon et al. 2008), though another intensive statewide survey is required to determine how many metapopulations and scrub-jays currently exist. One recent estimate suggests that there are currently between 6,000 and 9,000 scrub-jays remaining (~3,000 family groups; BirdLife International 2020). Management strategies such as prescribed fire and mechanical disturbance that promote an early successional, scrub-vegetation state can be used to preserve or grow scrub-jay populations (e.g., at ABS; Boughton and Bowman 2011). Such management likely would help to guard remaining metapopulations throughout the state against extirpation, though studying population trends at numerous sites beyond ABS and MINWR may help to identify where to focus conservation efforts and how those efforts should be fine-tuned based on location. To better understand scrub-jay metapopulations throughout the state, however, existing datasets that document population trends must be used effectively.

The metapopulation that includes scrub-jays at Seminole State Forest (SSF; 28.9 N, 81.5 W; metapopulation 18 in Stith et al. [1996]) in north-central Florida is >175 km to the north of ABS (27.1 N, 81.2 W) and >70 km west-northwest of MINWR (28.3 N, 80.4 W). This distance functionally precludes SSF scrub-jays from interbreeding with these well-studied scrub-jay groups (Coulon et al. 2008). Scrub-jays at SSF are genetically most similar to those at Ocala National Forest (ONF) and in metapopulations elsewhere in the western part of north central Florida, which are all a part of the largest genetic group—based on geographic coverage—identified by Coulon et al. (2008; Fig. 1). Studies at SSF could improve our understanding of scrub-jays in the understudied region wherein the property occurs and could be compared to studies completed at ABS or MINWR to determine the applicability of those studies to other metapopulations, and so optimize conservation efforts. The population of scrub-jays at SSF has been monitored since 2008 and exemplifies an opportunity to effectively use an existing dataset to better understand population trajectory. The viability of the SSF scrub-jay population could possibly be used as an indicator for the viability of the metapopulation that it prominently exists within, though monitoring of populations outside of SSF would be required to confirm this possibility. Determining scrub-jay population viability at SSF could also indicate if management practices implemented there,



**Figure 1.** Sites where scrub-jays occur that are discussed herein: S = Seminole State Forest, O = Ocala National Forest, M = Merritt Island National Wildlife Refuge, and A=Archbold Biological Station. The locations of these letters (which do not correspond to polygons) indicate the center of the sites described. Major solid lines outlining polygons indicate the most biologically likely scrub-jay genetic groups as identified by Coulon et al. (2008). Minor solid lines indicate county boundaries and light gray shading indicates waterbodies.

or at locations where similar management techniques are being used, should be modified to increase the likelihood of long-term scrub-jay persistence. Additionally, demonstrating the usefulness of long-term scrub-jay population data for projecting future population change could inspire such analysis of similar datasets to help inform management decisions. Therefore, our objectives were to report SSF population survey data from 2008 to 2016 and to use only these data to estimate population viability of the scrub-jay population at SSF using a simple analysis that managers could easily implement elsewhere.

## METHODS

*Study site.*—Since being established in 1990 in Lake County, Florida, SSF has expanded to include approximately 113 km<sup>2</sup>. Approximately 6 km<sup>2</sup> of this area is xeric scrub dominated by sand live oak (*Quercus geminata*), myrtle oak (*Quercus myrtifolia*), and sand pine (*Pinus clausa*) currently in suitable condition (Woolfenden and Fitzpatrick 2020) for scrub-jay occupation and reproductive success at population replacement levels (R. Risch, Florida Forest Service, pers. obs.). Other land cover types that occur on the property, among which scrub is interspersed, include upland pine forests (e.g., slash pine [*Pinus elliottii*], long leaf pine [*Pinus palustris*]) and riparian vegetation (e.g., sabal palm [*Sabal palmetto*], pond pine [*Pinus serotina*]) along Blackwater Creek and its tributaries within the Wekiva River Basin. Existing scrub vegetation is maintained via prescribed fire. The greater SSF area (including a state park and state reserve) is bordered on the east, south, and west by dense human settlement including the Orlando metropolitan area. The southeastern part of ONF borders SSF on the north and is where the nearest concentration of scrub-jays occurs, though the approximate number of scrub-jays in the southeast part of ONF is unknown.

*Population surveys.*—Between 2008 and 2016, population surveys occurred on average eight times per year (every six weeks) in March, April, June, July, September, October, and December. Each year, the majority of the scrub-jays present were banded with unique combinations of colored bands and trained to approach the surveyor upon hearing a whistle (80–90% of scrub-jays were typically banded at any time). The surveyor searched all suitable scrub patches at SSF (i.e., those 5–15 years post-burn) for scrub-jays during a one-week period during each population survey. Scrub patches outside of the 5–15 years post-burn range were rarely used and surveyed only if scrub-jays were known to use those sites based on daily work responsibilities of the surveyor at the property. Scrub-jays were attracted to the playback of conspecific vocalizations broadcast by the same surveyor each year. The surveyor counted both the number of all-purpose territories defended by at least one bird—these territories tended to be spatially stable through time—and the number of scrub-jays. Surveys typically lasted 2–20 minutes, depending on how quickly the surveyor identified individuals documented at the territory during previous surveys. The surveyor did not conduct surveys when aerial predators were present. During surveys, the surveyor broadcast conspecific audio from locations throughout the focal territory until they observed the focal individuals. This process also occurred at scrub patches that the experienced surveyor believed had a reasonable chance of containing scrub-jays but where recent, previous surveys had not indicated scrub-jay presence. The surveyor re-visited territories where they had previously documented scrub-jays but did not observe scrub-jays during the first survey; they re-visited the territory at least twice to confirm absence. This same process (two re-visits) occurred for missing breeding individuals, and for missing helpers, at least one re-visit occurred (the scrub-jay cooperative breeding system is described by Woolfenden and Fitzpatrick [1984]). The surveyor completed all surveys in a one-week period to minimize the risk of double-counting due to movement of un-banded individuals. Further, the scrub-jays that were present tended to approach the surveyor, which minimized the likelihood of missing individuals. We are therefore confident that our counts of scrub-jay population size at SSF are accurate. We chose to report data only from the March population survey herein, and to base our analysis on these data, because this survey was the least likely to miss un-banded individuals such as juveniles (yet to be trained to approach the surveyor), incubating or brooding individuals, or recent immigrants.

*Population viability analysis (PVA).*—Using the counts of scrub-jays in March between 2008 and 2016, we calculated population change ( $\lambda$ ), which indicates how the SSF population size ( $N$ ) changed from one year ( $t$ ) to the next ( $t+1$ ):

$$\lambda = \frac{N_{t+1}}{N_t}$$

A  $\lambda$  value for 2008 of 0.91, for example, indicates that between March of 2008 and March of 2009, the total number of scrub-jays at SSF declined by 9%.

We used a discrete model to predict temporal population change:

$$N_{t+1} = \lambda \times N_t$$

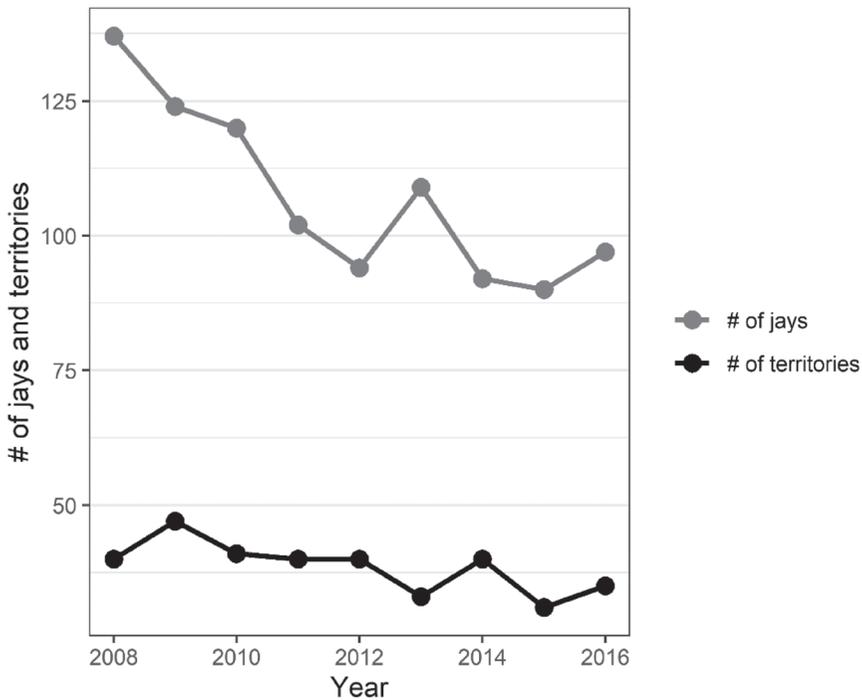
We used this model to project population change 100 years into the future based on random selection of a  $\lambda$  value for each year for 10,000 populations. We randomly selected the  $\lambda$  values from a log-normal distribution (the best fit for the observed  $\lambda$  values) that was structured based on the mean and standard deviation (SD) that we calculated using the natural log of each observed  $\lambda$  value from 2008 to 2015. Each simulated population began at the mean population size observed from 2008 to 2016 (107). Though we did not model environmental and demographic stochasticity explicitly, we assumed that the natural variation in  $\lambda$  that we simulated accounted for the majority of these factors (effects of future climate change, however, are absent).

We estimated probability of extirpation for the SSF population based on the proportion of the 10,000 simulated populations that declined to below 3 individuals during the 100-year simulation. We chose this threshold for extirpation because less than 3 individuals would be smaller than the mean observed family size at SSF during our study period (2.8) and would indicate that breeding success had likely ceased or would soon.

We also estimated how different long-term means of yearly  $\lambda$  values for the SSF population might affect extirpation probability and population size. To do so, we systematically increased the mean  $\lambda$  value from the observed 0.96 by iteratively adding 0.01, 0.02, 0.03, and 0.04 to all observed yearly (2008 to 2015)  $\lambda$  values, calculated the natural log for each of those sets of derived values, and then calculated the mean and standard deviation to conduct a PVA as described above. Then we determined which artificially increased mean  $\lambda$  values (of 0.97, 0.98, 0.99, and 1.00) resulted in at least 95% of the simulations not ending in extirpation (i.e.,  $N \geq 3$  after 100 years). We conducted analyses in R (v. 3.6.2; R Core Team 2019). Variability reported is standard deviation unless otherwise noted.

## RESULTS

Between 2008 and 2016, mean population size in March at SSF was  $107.22 \pm 16.47$  (Fig. 2). The population size ranged from a high in 2008 of 137 to a low in 2015 of 90 and ended at 97 individuals in 2016 (Fig. 2). During the study period, the 8  $\lambda$  values for population size had a mean of  $0.96 \pm 0.11$  and tended to decline temporally (6 of 8  $\lambda$  values indicated a decline; Fig. 3). Mean number of territories in March was  $38.56 \pm 4.82$  (Figs. 2, 4) and the 8 associated  $\lambda$  values for territories had a mean of  $1.0 \pm 0.16$  (4 indicated a decline; Fig. 3). The  $\lambda$  values for number of scrub-jays and number of territories did not tend to vary synchronously with respect to degree or direction of change (Fig. 3). Mean scrub-jays per territory in March was  $2.79 \pm 0.39$ , tended to decline temporally (5 of 8 transitions), and also did not tend to vary in the same direction as number of territories through time (Fig. 4). We did not detect a significant correlation between number of territories and number of scrub-jays per territory ( $r = -0.288$ ,  $df = 7$ ,  $P = 0.45$ ), though sample size and power were low such that an undetected negative relationship is possible.

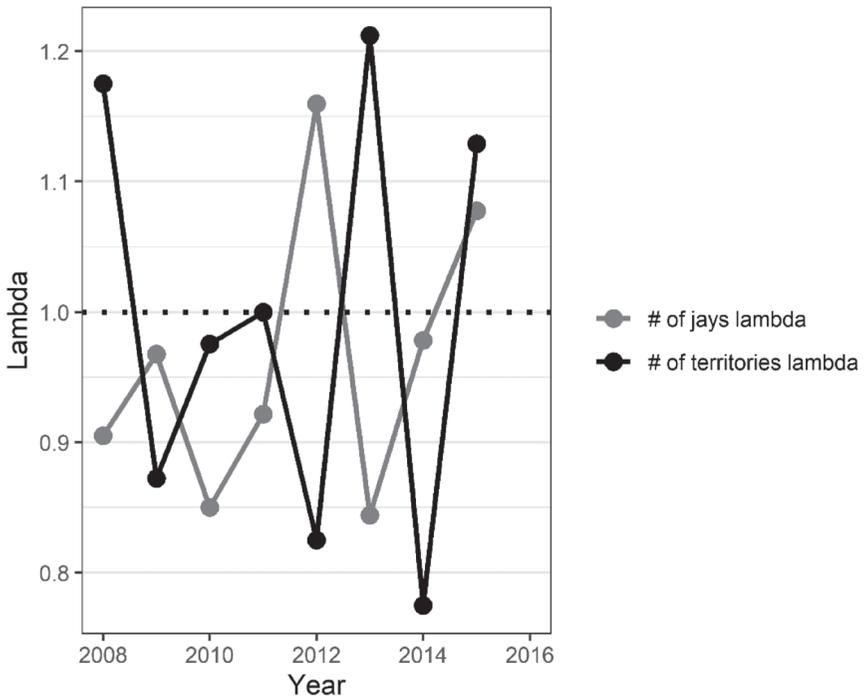


**Figure 2.** Variation in number (#) of scrub-jays (gray) and number of territories (black) at Seminole State Forest between 2008 and 2016 during the March population survey.

The range of  $\lambda$  values observed between 2008 and 2015 resulted in an extirpation probability within 100 years of 0.78 (Fig. 5). Upon systematically increasing the mean of yearly  $\lambda$  values for our study period, we found that mean  $\lambda$  values of 0.97, 0.98, 0.99, and 1.00 resulted in extirpation probabilities of 0.44, 0.14, 0.02, and 0.00, respectively (Fig. 5). With increasing  $\lambda$ , projected final population sizes tended to increase and median year of extirpation tended to occur later (Table 1).

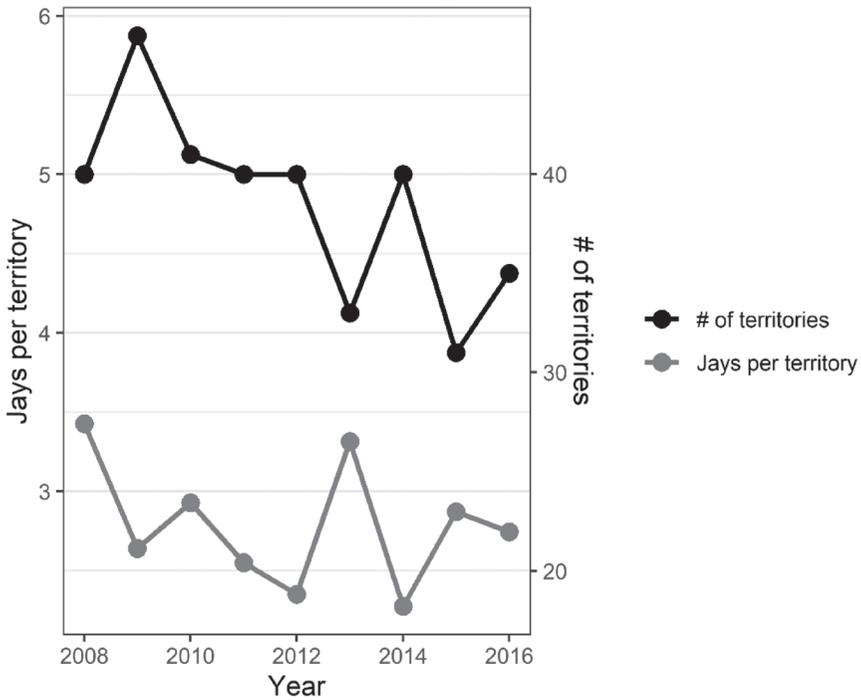
## DISCUSSION

Based on the generally declining number of scrub-jays that occurred at SSF between 2008 and 2016 (Figs. 2, 3), our PVA indicated that the SSF population has a 0.78 extirpation probability within the next 100 years (Fig. 5) if the range of  $\lambda$  levels that we observed is representative of future conditions. The number of territories at SSF were relatively constant during the study period (Figs. 2, 4) compared to the period between 1992 and 2010 when the number of territories more than doubled (Boughton and Bowman 2011). Both number of



**Figure 3.** Variation in population change (lambda) values for number (#) of scrub-jays (gray) and number of territories (black) at Seminole State Forest between 2008 and 2015, based on March population surveys. The horizontal dashed line represents no growth. The lambda values for number of scrub-jays and for number of territories tended to vary in the opposite direction.

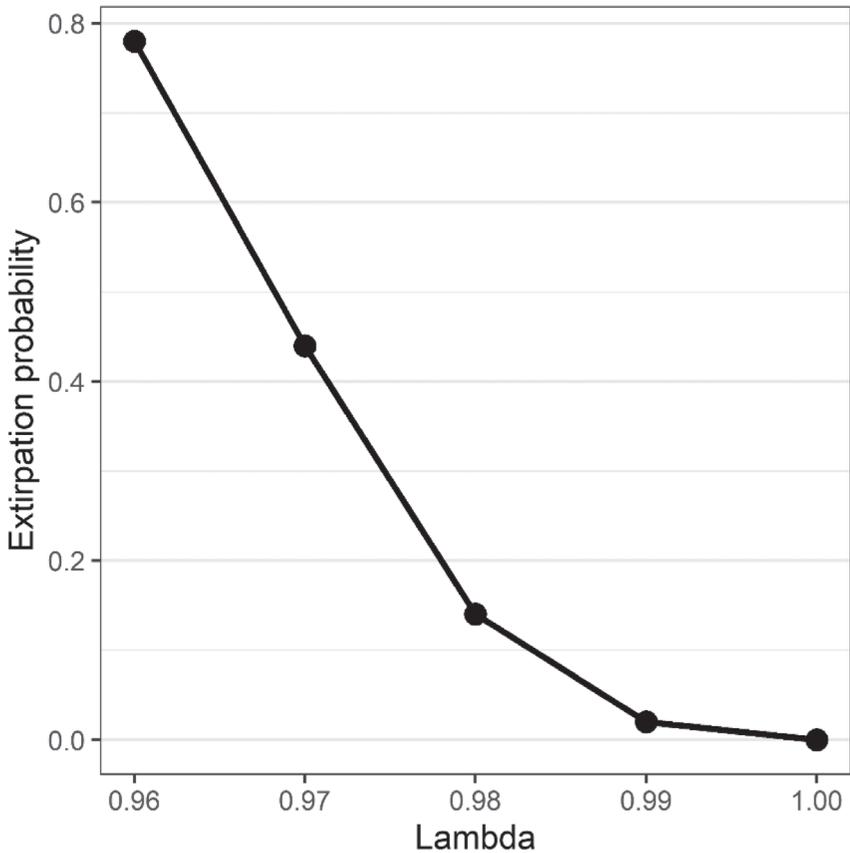
territories and number of scrub-jays per territory did, however, tend to decline during the study period and generally varied between years in opposite directions (Fig. 4). We also observed that between-year changes in total scrub-jays and territory numbers at SSF often varied in opposite directions (Figs. 2, 3). The cooperative breeding system of scrub-jays (Woolfenden and Fitzpatrick 1984), in which some juveniles remain helpers on parental territories, could explain both of these patterns (Figs. 2, 3, 4). Fewer scrub-jays per territory would be expected when there are more territories resulting from dispersal and vice versa (Fig. 4). Opposite trajectories in overall scrub-jay population and territory number (Figs. 2, 3) could indicate an oscillation between productive years when habitat is saturated (juveniles survive because of favorable conditions but do not disperse because of lack of suitable habitat available) and mortality-mediated habitat availability, which facilitates territory establishment by former helpers. Productive years and saturated habitat might result in larger territories with more



**Figure 4.** Mean number of scrub-jays per territory at Seminole State Forest (gray; left y axis) and number of territories (black; right y axis) during March population surveys from 2008 to 2016. The number of territories and number of scrub-jays per territory tended to vary in the opposite direction.

scrub-jays per territory (and more scrub-jays overall, fewer territories), whereas habitat vacated by deceased breeders might result in colonization by former helpers that establish smaller, less scrub-jay-dense territories (and fewer scrub-jays overall, more territories).

Regardless, it is clear that the SSF scrub-jay population, and perhaps the metapopulation to which it belongs, requires modified management action to improve conditions to attain a reasonably low extirpation probability (e.g.,  $< 0.05$ , acceptable risk) within the next 100 years. An additional 18 km<sup>2</sup>, approximately, of xeric-scrub could be restored at SSF as habitat for scrub-jays. Even moderate expansion of area managed as scrub-jay habitat within SSF boundaries could possibly, if targeted around patches with high scrub-jay densities (Breininger et al. 2006), be sufficient to increase the mean  $\lambda$  value on the property from 0.96 to 0.99 or greater and so significantly reduce extirpation probability (Fig. 5). Our simulations suggest that such a modest increase in  $\lambda$  could reduce extirpation risk to acceptable



**Figure 5. Projected extirpation probabilities during a 100-year period as a function of different mean values of population change (lambda) for the Seminole State Forest scrub-jay population. The mean lambda value observed between 2008 and 2015 was 0.96 and extirpation probabilities are based on the proportion of 10,000 simulations that resulted in extirpation.**

levels at SSF and perhaps for the entire metapopulation, given that most of its scrub-jays are assumed to exist in SSF. Further, modifying the frequency of prescribed fire or mechanical removal of larger trees in existing scrub could improve the quality of habitat and so increase scrub-jay numbers (Breininger et al. 2014, Woolfenden and Fitzpatrick 2020). We did not conduct habitat surveys during this study; therefore, we do not know the primary driver of population change at SSF. Regardless, our results suggest that conservation funds meant to benefit scrub-jays would, in conjunction with habitat surveys, likely be well-spent on conducting management activities at SSF.

**Table 1. Mean final scrub-jay population size and standard error (SE), median years until extirpation, and years until first extirpation based on 10,000 simulations for different mean values of population change ( $\lambda$ ). Each simulation had a duration of 100 years. The mean  $\lambda$  value observed at Seminole State Forest between 2008 and 2015 was 0.96.**

$\lambda$	Mean final population size (SE)	Median years until extirpation	Years until first extirpation
0.96	1.67 (0.04)	75	28
0.97	6.44 (0.11)	85	37
0.98	20.02 (0.31)	88	41
0.99	55.26 (0.78)	89	49
1.00	150 (2.13)	89	65

A limitation of our PVA is that it did not explicitly consider environmental or demographic stochasticity or density dependence but rather relied on the variation in observed  $\lambda$  values to encapsulate such processes. Regarding catastrophes, we believe that our approach is justifiable given that SSF is distant from the coast, which causes the catastrophic effects of hurricanes to generally be avoided. Epidemics, however, can substantially increase extirpation probability (Breininger et al. 1999) and exemplify a stochastic event that may not have occurred during our study period that could occur in the future. Similarly, wildfires could also occur and may increase in frequency and severity because of climate change. We believe, however, that the simplicity of our model is advantageous in that only population survey data are required, which, in many cases, is all that managers who wish to determine the trajectory of their population possess. As with all PVAs (Lacy 2019), but especially with respect to ours because of its simplicity, caution should be used when interpreting our results which are meant as a rough guide rather than an exact prediction about how SSF scrub-jay population size may change in the future. If scrub-jays are monitored for longer periods of time, the accuracy of analyses such as ours will likely improve.

Given that many of the remaining scrub-jay metapopulations are currently likely declining (Coulon et al. 2008, Boughton and Bowman 2011), it is crucial to identify which of these metapopulations could feasibly be conserved, which metapopulations require management modification, and which metapopulations could benefit from habitat acquisition. Monitoring efforts, such as Audubon Florida's Jay Watch community science (i.e., citizen science) program, can produce accurate population survey data (Miller et al. 2015) and could be expanded to other sites throughout Florida. These or similar data could be used to complete periodic viability analyses, as demonstrated by the current study, for each remaining metapopulation to help inform decision

makers about where limited conservation resources would be most effectively allocated. Though he used a more complex (individual-based, spatially explicit) viability analysis than the one described herein, Stith (1999) completed an analysis of metapopulation viability previously. Another such effort could help to identify areas of current conservation need and also help managers to identify which scrub-jay populations are being managed in a way that can sustain scrub-jays and should be emulated. Our approach could feasibly be incorporated into a state-wide metapopulation analysis by providing a simple process by which to use site-specific scrub-jay population trend data that might otherwise remain largely unused. It will be important, however, to consider not just changes in  $\lambda$  but also to identify what factors (e.g., habitat management, genetic diversity) are influencing that metric of population change.

The Florida Scrub Working Group approach currently being employed helps to facilitate the communication required to achieve such state-wide goals. When possible, those seeking advice about scrub-jay habitat management techniques should prioritize consulting land managers at properties where scrub-jays within the same metapopulation (Stith et al. 1996), or at least the same genetic group (Coulon et al. 2008), have been successfully managed. For example, managers of scrub-jay habitat in the Northeast Florida Scrub Working Group region may benefit more from communicating with the managers at SSF than with managers in other parts of the state given regional variation in scrub types and re-growth rates. This collaborative, biologically informed approach among managers based on which metapopulation or genetic group is being managed, rather than being based solely on which species is being managed, could both improve our ability to conserve scrub-jays and serve as a model for conserving other sedentary, range-restricted species.

#### ACKNOWLEDGMENTS

We thank Florida Forest Service employees Joe Bishop (Forestry Supervisor II) and Mike Martin (Forester) for their work at Seminole State Forest and for their years of support for and assistance with scrub-jay management efforts. Karl E. Miller provided helpful advice during manuscript preparation. Kevin L. Pangle provided R code in support of the population viability analysis, and helpful instruction. Two anonymous reviewers helped to improve the manuscript. This research was supported by the Earth and Ecosystem Science PhD program at Central Michigan University.

#### LITERATURE CITED

BIRDLIFE INTERNATIONAL. 2020. *Aphelocoma coerulescens*. The IUCN Red List of Threatened Species 2020:e.T22705629A179678639.

- BOUGHTON, R., AND R. BOWMAN. 2011. State-wide assessment of Florida Scrub-jays on managed areas: a comparison of current populations to the results of the 1992-93 survey. U.S. Fish and Wildlife Service, Washington, D.C., USA.
- BREININGER, D. R., M. A. BURGMAN, AND B. M. STITH. 1999. Influence of habitat quality, catastrophes, and population size on extinction risk of the Florida Scrub-jay. *Wildlife Society Bulletin* 27:810–822.
- BREININGER, D. R., E. D. STOLEN, G. M. CARTER, D. M. ODDY, AND S. A. LEGARE. 2014. Quantifying how territory quality and sociobiology affect recruitment to inform fire management: recruitment in fire-maintained ecosystems. *Animal Conservation* 17:72–79.
- BREININGER, D. R., B. TOLAND, D. M. ODDY, AND M. L. LEGARE. 2006. Landcover characterizations and Florida Scrub-jay (*Aphelocoma coerulescens*) population dynamics. *Biological Conservation* 128:169–181.
- COULON, A., J. W. FITZPATRICK, R. BOWMAN, B. M. STITH, C. A. MAKAREWICH, L. M. STENZLER, AND I. J. LOVETTE. 2008. Congruent population structure inferred from dispersal behaviour and intensive genetic surveys of the threatened Florida Scrub-jay (*Aphelocoma coerulescens*). *Molecular Ecology* 17:1685–1701.
- FAHRIG, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management* 61:603–610.
- HARNIK, P. G., C. SIMPSON, AND J. L. PAYNE. 2012. Long-term differences in extinction risk among the seven forms of rarity. *Proceeding of the Royal Society B* 279:4969–4976.
- LACY, R. C. 2019. Lessons from 30 years of population viability analysis of wildlife populations. *Zoo Biology* 38:67–77.
- MILLER, K. E., C. A. FAULHABER, AND J. O. GARCIA. 2015. Accuracy assessment of a Jay Watch post-reproductive survey of Florida Scrub-jays (*Aphelocoma coerulescens*). *Florida Field Naturalist* 43:139–145.
- MILLER, K. E., AND B. M. STITH 2002. Florida Scrub-jay distribution and habitat in Charlotte County. Center for Avian Conservation, Inc., Gainesville.
- OWENS, I. P. F., AND P. M. BENNETT. 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proceedings of the National Academy of Sciences* 97:12144–12148.
- R CORE TEAM. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- SIMBERLOFF, D. 1995. Habitat fragmentation and population extinction of birds. *Ibis* 137:S105–S111.
- STITH, B. M. 1999. Metapopulation dynamics and landscape ecology of the Florida Scrub-jay, *Aphelocoma coerulescens*. Dissertation, University of Florida, Gainesville.
- STITH, B. M., J. W. FITZPATRICK, G. E. WOOLFENDEN, AND B. PRANTY. 1996. Classification and conservation of metapopulations: a case study of the Florida Scrub Jay. Pages 187–215 in *Metapopulations and wildlife conservation* (D. R. McCullough, Ed.). Island Press, Washington, D.C.
- WHITLOCK, M. C. 2000. Fixation of new alleles and the extinction of small populations: drift load, beneficial alleles, and sexual selection. *Evolution* 54:1855–1861.
- WOOLFENDEN, G. E., AND J. W. FITZPATRICK. 1984. The Florida Scrub Jay: demography of a cooperative-breeding bird. Princeton University Press, Princeton, New Jersey.
- WOOLFENDEN, G. E., AND J. W. FITZPATRICK. 2020. Florida Scrub Jay (*Aphelocoma coerulescens*), version 1.0. In *Birds of the World* (A. F. Poole and F. B. Gill, Eds.). Cornell Lab of Ornithology, Ithaca, New York.