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New insights from an attempt to reintroduce Red-cockaded Woodpeckers in northern Florida

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ABSTRACT. Red-cockaded Woodpeckers (*Leuconotopicus borealis*) were extirpated from Tall Timbers Research Station in the early 1980s. To help meet conservation goals established for this imperiled species in north Florida, we attempted to reintroduce the woodpecker to the research station by constructing artificial cavities and translocating 27 subadult woodpeckers from 2006 to 2010. Successful nesting occurred during the breeding season following the initial translocation of four male–female pairs. Translocations were suspended in 2011 when breeding groups occupied 6 of 12 available clusters of cavity trees. The population increased steadily after 2011 and, in 2015, totaled 28 adults distributed among nine breeding groups plus a single territorial male. The 2015 population included 22 individuals produced at Tall Timbers, an immigrant female, and five birds originally translocated as subadults. Seven breeding groups in 2015 also had non-breeding helpers. New milestones documented during this reintroduction attempt included recruitment of locally produced birds into the breeding population, excavation of natural cavities, two immigration events, and natural expansion into an unoccupied area. We also documented the threat that heavy rains may pose to small populations. Expenses totaled $211,000 during the first 5 yr when translocations and cavity construction were the primary activities. After translocations were suspended, recurring management expenses were ~ $6500 annually. Because our founding population was small ($N = 12$), intermittent translocations will likely be needed in the future to offset the deleterious effects of inbreeding.

RESUMEN. **Nuevas perspectivas en el intento de reintroducir a *Leuconotopicus borealis* en el norte de Florida**

El Carpintero (*Leuconotopicus borealis*) fue extirpado de la estación de investigación Tall Timbers temprano en los 1980s. Para ayudar a lograr las metas de conservación establecidas para este carpintero, en el norte de Florida, intentamos reintroducir el ave en la estación de investigación construyendo cavidades artificiales y translocando 27 sub-adultos, desde el 2006 al 2010. Luego de la translocación inicial de cuatro parejas, hubo anidamiento exitoso, durante la época de reproducción. La reintroducción de aves se detuvo en el 2011, cuando los grupos reproductivos ocuparon seis de las 12 congregaciones de cavidades en árboles. Luego del 2011, la población aumentó y en el 2015, había 28 adultos distribuidos entre nueve grupos reproductivos, además de un macho solitario que estableció un territorio. La población del 2015 incluía 22 individuos nacidos en Tall Timbers, una hembra inmigrante y cinco de las aves reintroducidas originalmente como sub-adultos. Siete de los grupos reproductivos en el 2015 contenían ayudantes. Nuevos hitos documentados durante este intento de reintroducción incluyó, el reclutamiento de individuos nacidos en la localidad, el producir cavidades naturales, dos eventos de inmigración y la expansión natural de las aves a áreas previamente no ocupadas. También documentamos la amenaza que representan fuertes lluvias en una población pequeña. Se utilizaron $211,000 durante los primeros cinco años cuando las translocaciones y la construcción de cavidades fue la principal actividad. Luego de las translocaciones, los gastos de manejo fueron unos $6,500 anuales. Dado el caso de que la población de fundadores fue pequeña ($N = 12$), en el futuro se necesitaran translocaciones, de forma intermitente, para evitar los efectos negativos de la endogamia.

Key words: artificial cavities, *Leuconotopicus borealis*, translocation, tropical storm

Red-cockaded Woodpeckers (*Leuconotopicus borealis*) are endemic to mature pine forests of the southeastern U.S.A (Jackson 1994). Their ecology is shaped by the excavation of nest and roost cavities only in mature (>80 yr old) living pine trees coupled with habitat conditions best maintained by frequent fire (Jackson 1994). Excavation of natural cavities can take years to complete, and availability of suitable cavity resources affects occupancy, dispersal, and many key behaviors (Walters et al. 1992, Pasinelli and Walters 2002). Cavities excavated by Red-cockaded Woodpeckers also are used by many other species (Blanc and Walters

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2008a), and these qualities make the woodpecker both a keystone cavity excavator in southern pine forests as well as an important indicator of mature, well-managed forests (Jackson 1994, Blanc and Walters 2008a).

Many populations of Red-cockaded Woodpeckers have stabilized or increased in recent years (Lammertink 2014). These positive trends reverse largely negative trends documented in previous decades (Ligon et al. 1986) and are linked to improved silvicultural and fire management as well as two procedures now used to manage many populations (Costa and DeLotelle 2006). First, construction of artificial cavities can help overcome a scarcity of suitable natural cavities (Copeyon 1990, Allen 1991) and, second, translocation of subadult woodpeckers can augment small, isolated populations and mitigate the possible negative effects of isolation and fragmentation (Edwards and Costa 2004, Rudolph et al. 2004). Although recovery goals for Red-cockaded Woodpeckers include self-sustaining populations that are not wholly dependent on artificial cavities and translocation (USDI 2003), these tools have helped sustain small, isolated populations as well as larger populations where forest conditions are not yet suitable (Costa and DeLotelle 2006).

Artificial cavities and translocation also represent the tools needed to reintroduce Red-cockaded Woodpeckers to formerly occupied areas (Hagan et al. 2004a). The first such reintroduction attempted in 1998 involved excavation of 87 artificial cavities and translocation of 20 subadult male–female pairs (Hagan et al. 2004a). The attempt was considered successful when the reintroduction site supported 10 territories (Hagan et al. 2004a), but no information has been published describing the growth and stability of this population since translocations were suspended in 2001. Details regarding the habitat conditions at the release site, times when important milestones occurred (e.g., excavation of natural cavities, immigration, and recruitment of locally produced young into the population), and overall costs were also not documented. Similar information gaps exist for other reintroduction attempts ($N = 7$; R. Costa, pers. comm.) even though such information is essential for comparing the progress and success of reintroduction efforts (Sutherland et al. 2010).

Red-cockaded Woodpeckers occurred on Tall Timbers Research Station (TTRS) from at least the early 1940s through the early 1980s (Baker 1983). TTRS supported 11 potential breeding groups (PBGs, a preferred population metric for this cooperatively breeding species; USDI 2003) in 1970, but the population declined and eventually disappeared in 1981. Baker (1983) listed three potential causes for the extirpation: (1) inbreeding depression brought on by population isolation, (2) reductions in habitat quality as a result of midstory hardwood encroachment, and (3) the dominance of loblolly (*Pinus taeda*) and shortleaf (*Pinus echinata*) pines on TTRS. Inbreeding was suspected by Baker (1983) because the nearest PBG was >5 km from TTRS at the time the population vanished; natal dispersal distances for this species are usually <3 km (Daniels and Walters 2000). Hardwood midstory increased on TTRS in part through the establishment of research plots ($N = 84$) where fire frequency was manipulated (Crawford et al. 2012). For example, one PBG may have been eliminated by hardwood encroachment when fire was permanently excluded from a 10-ha area beginning in 1967. The research plot encompassed many of the cavity trees available to this PBG (Engstrom et al. 1984). Finally, Baker (1983) suggested that the quality of shortleaf and loblolly cavity trees declined as they aged.

Population reintroduction is appropriate to consider when the causes of extirpation can be managed or eliminated (Griffith et al. 1989). A hardwood harvest conducted in 1999 removed >85% of the fire research plots and reduced hardwood midstory throughout TTRS. Afterwards, greater emphasis was placed on burning upland pines at least every other year (E. Staller, pers. comm.). These changes provided an open forest structure that appeared capable of sustaining a reintroduced population. Furthermore, if a reintroduced population was established, threats posed by inbreeding depression or deteriorating cavity resources could be managed using additional translocations and cavity construction (Costa and DeLotelle 2006).

We attempted to reintroduce Red-cockaded Woodpeckers to TTRS starting in 2006. If successful, the reintroduction would help satisfy population goals for the Red Hills region

($N \geq 25$ PBGs; ~ 20 PBGs in 2006) established in Florida's woodpecker management plan (FFWCC 2003) and could potentially provide new information about the reintroduction process. Our objectives here are to provide new and more comprehensive details about a reintroduction attempt for Red-cockaded Woodpeckers by describing (1) forest conditions at the reintroduction site, (2) the placement of artificial cavities and other reintroduction procedures, (3) population growth before and after translocations were suspended, (4) the occurrence of important milestones, and (5) the cost of the reintroduction effort. This information comports with recent standards recommended for monitoring avian reintroductions and will help others plan for and assess other attempts to reintroduce this imperiled species to former parts of their range (Sutherland et al. 2010).

METHODS

Tall Timbers Research Station (30°29′N 84°32′W) is located in the Red Hills physiographic region of northern Florida and southern Georgia (Cox et al. 2001). Upland areas on TTRS were used primarily for agriculture until the early 1900s and became reforested as land-use shifted toward management of forest and wildlife resources (Crawford et al. 2012). Loblolly and shortleaf pines colonized agricultural areas following abandonment of agricultural operations (Baker 1983). Dominant canopy trees in the old-field pinelands on TTRS were >80 yr old at the time the reintroduction attempt was initiated.

Habitat quality and population goals. Old-field pine forests on TTRS encompassed 854 ha. Habitat quality was assessed using 0.04-ha plots ($N = 2576$) distributed systematically every 60 m throughout upland pine forests (S. Wellendorf, unpubl. data). Species and diameter at breast height (DBH) were recorded for each tree in a plot, and these data were used to calculate the number of criteria satisfied for seven attributes found in the recovery standard for Red-cockaded Woodpecker foraging habitat (USDI 2003; Table 1). Frequent burning and removal of hardwoods in 1999 created conditions that satisfied the four remaining attributes used to assess foraging habitat (Table 1). Next, we used the 0.04-ha sample plots and a geographic information system (GIS; ESRI 2006) to create a 30 × 30-m grid depicting habitat quality. We averaged the number of foraging criteria satisfied for the 0.04-ha sample plots within 120 m of each grid cell and assigned this value to the cell (Fig. 1).

Tall Timbers Research Station appeared capable of supporting 10–12 PBGs based on the number historically present and typical densities elsewhere in the Red Hills region with similar habitat conditions (40–80 ha^{-1}; Cox et al. 2001). Because individual PBGs

Table 1. Foraging habitat guidelines provided in the Red-cockaded Woodpecker recovery plan (USDI 2003). Forest characteristics for pine basal area (BA) and pine stem densities were measured on 0.04-ha samples distributed systematically throughout upland pine habitat ($N = 2576$). Values under percent satisfied reflect the percent of 0.04-ha sample plots on Tall Timbers Research Station that satisfied the individual criteria listed in the guidelines.

Forest characteristic	Federal guideline	Percent satisfied
Density of large pines	>45 stems/ha > 35 cm DBH	36.5
BA for large pines	>35 cm DBH > 4.6 m^2/ha	52.1
BA for medium pines	25.4–35 cm DBH < 9.2 m^2/ha	35.5
BA for small-to-medium pines	<25.4 cm DBH < 2.3 m^2/ha	48.5
Density of small-to-medium pines	<50 stems/ha for stems < 25.4 cm DBH	41.9
BA all pines >25.4 cm dbh	>9.2 m^2/ha	38.2
Ground cover conditions	>40% grass and forbs	100.0
Hardwood midstory	<2.1 m^2/ha	100.0
Canopy hardwoods	<30% number of canopy trees	57.0
Habitat dispersion	<0.8 km	100.0
Contiguous habitat area	50% within 400 m	100.0

DBH, diameter at breast height.

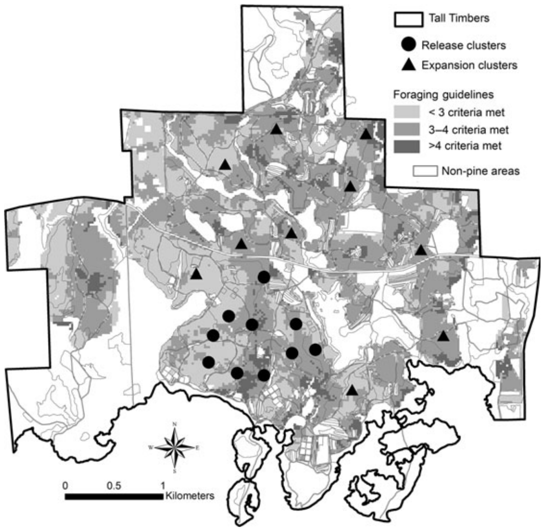

Fig. 1. Upland pine forests on Tall Timbers Research Station and their compliance with the selected criteria established for recovery-standard foraging guidelines (Table 1). Forest characteristics were quantified using 0.04-ha sample plots distributed systematically throughout upland pines ($N = 2576$). An interpolated grid was then created in a geographic information system using the number of foraging criteria satisfied by each sample and the 4–6 neighboring samples within 120 m.

frequently include non-breeding helpers (Walters et al. 1988), this target population might contain 20–30 adult woodpeckers at maximum occupancy. Population viability models suggest highly aggregated PBGs containing 20–30 adults have a good chance of persisting for 25 yr (Walters et al. 2002). The recurring management we proposed should enhance chances of population persistence. Annual management included maintenance of suitable habitat conditions throughout upland pines using prescribed fires with a ≤2-yr fire-return interval. We also monitored cavity resources, nesting activity, and the number of breeding groups present annually, and replaced artificial cavities as needed at least every other year.

Recruitment cluster characteristics and placement. Recruitment clusters each initially contained four artificial insert cavities (Allen 1991) installed >8 m above ground (USDI 2003). Construction of recruitment clusters involved a two-phased approach that consisted of initial establishment in a small portion of TTRS (phase one) and post-establishment expansion throughout appropriate habitat (phase two). During the first phase of cavity construction, we established 10 recruitment clusters in a 250-ha area on the southern half of TTRS (release clusters in Fig. 1). The density of recruitment clusters ($\sim$ 25 ha^{-1}) was higher than natural territory densities in the region (40–80 ha^{-1}; Cox et al. 2001), and the rationale for the concentration was to (1) provide an area where ≥1 PBG might initially establish, (2) ensure that translocated subadult woodpeckers encountered artificial cavities after release, and (3) promote social interactions (Carrie et al. 1999).

A second phase of recruitment cluster construction was initiated once at least one PBG became established in the 250-ha phase-one area. We constructed 10 additional recruitment clusters (expansion clusters in Fig. 1) outside the phase-one area that were separated by $\sim$ 500 m (the average distance between natural PBGs in the Red Hills region; Cox et al. 2001). The overall population goal of 10–12 PBGs could be achieved if 1–2 recruitment clusters in the phase-one area were occupied and 8–10 recruitment clusters in the phase-two area were also occupied. In addition, we proposed to increase cavity resources once a recruitment cluster was occupied. Augmentation included installing two additional artificial cavities (for a total of six per cluster) and two drilled advanced starts. The advanced starts consisted of an entrance tunnel with an enlarged chamber at the end of the tunnel (USDI 2003) that could promote cavity excavation by resident individuals. We also added two additional advanced starts in each occupied cluster in 2015.

Population monitoring and translocation. The Red Hills population located northeast of TTRS (Cox et al. 2001) was the primary source of subadult woodpeckers ($N = 23$). From 2006 to 2009, we uniquely color-marked 37–89 nestlings each year from 22 to 63 breeding groups. Nest monitoring, banding and sexing offspring, selection of subadults for translocation, capture and transport of subadults, and other field procedures followed federal guidelines (USDI 2003) and were conducted under permits TE142806-0 (U.S. Fish and Wildlife Service), 22446 (U.S. Geological Survey), LSSC-10-00134 and WB08121 (Florida Fish and Wildlife Conservation Commission), and 9139 (Georgia Department of Natural Resources). Additional translocated subadults ($N = 4$) were provided by Eglin Air Force Base (30°42′N 86°48′W; Okaloosa and Santa Rosa counties, FL) in 2010.

Translocations were performed from September to November, with most after mid-October to avoid periods when many migratory raptors move through the region (Crawford 1978). During phase one of the reintroduction, marked subadult males and females from different natal territories were paired, transported to TTRS, and placed in artificial cavities in TTRS recruitment clusters. A screen mesh placed over entrances held subadults in cavities until screens were removed at dawn. We also visited the initial release area weekly in 2006 to determine the presence/absence of the first cohort of translocated subadults.

Phase two of the reintroduction began in 2008. Subadults were released at occupied and unoccupied recruitment clusters following guidelines provided by DeFazio et al. (1987). The guidelines recommend that single males and male-female pairs be released in unoccupied clusters and females be paired with solitary males. We did not closely monitor the subadults released after 2006 and instead used retention of subadults into the following breeding season (mid-April) as the measure of translocation success (Carrie et al. 1999). Marked individuals associated with breeding groups were identified during each nesting season (USDI 2003), and we also used the number of nestlings banded at each nest as a measure of group productivity (Garabedian et al. 2014). We also looked for natural cavity excavations elsewhere on TTRS while conducting other field studies and monitored progress made on advanced starts in each recruitment cluster annually.

Statistical analyses. We used land-cover features and recovery foraging guidelines surrounding recruitment clusters (Fig. 1) to assess the influence that habitat conditions had on cluster occupancy. We defined stable clusters as those occupied by breeding groups for ≥2 yr ($N = 8$) and unstable clusters as clusters constructed in phase two of the reintroduction that (1) were never occupied or (2) were used by a PBG for <2 yr before the group moved permanently to another recruitment cluster ($N = 5$). Land-cover information derived from high-resolution aerial photographs (E. Staller, unpubl. data) was used in GIS to calculate the area of upland pine foraging habitat within 300 m of recruitment clusters. Fields, forested wetlands, stands of young pine (<30 yr), and other cover types were classified as non-foraging habitat following federal guidelines (USDI 2003). We also calculated the area within 300 m of recruitment clusters that satisfied <3, 3–4, and >4 foraging criteria using the 30-m^2 grid (Fig. 1). A non-parametric Mann–Whitney U-test was used in Systat (2007) to assess relationships between habitat conditions and cluster stability. We also used a t-test in Systat (2007) to compare nest productivity on TTRS with productivity of other woodpecker groups in the Red Hills.

RESULTS

Initial establishment. Three individuals were observed regularly during the weekly surveys conducted after eight subadults were first released in 2006. The two males and lone female did not roost in the recruitment clusters where they were released, but a breeding pair formed and initiated a nest in mid-May (Table 2). The first nest in 2007 was taken by a predator, but a second nest

Table 2. Retention and population growth of Red-cockaded Woodpeckers at Tall Timbers Research Station (TTRS), 2006–2015. Retention reflects subadults released at TTRS and retained into the following breeding season. Immigrants arrived unassisted, helpers assisted established breeders, and single males occupied recruitment clusters, but failed to attract mates. Growth and productivity were monitored using the (1) number of potential breeding groups (PBG) present, (2) number of nestlings banded, (3) mean annual clutch size, (4) number of individuals banded as nestlings on site and observed in subsequent breeding seasons (local adults), and (5) total adult population.

Year	Released	Retained	Immigrants	Helpers	Single males	PBG	Nestlings banded	Mean clutch size	Local adults	Total adults
2006	8	–	–	–	–	–	–	–	–	–
2007	8	3	0	0	0	1	2	3.0	0	3
2008	2	7	0	1	0	4	7	3.3	1	11
2009	5	2	0	1	0	2	5	3.3	3	6
2010	4	2	1	2	0	4	7	2.8	5	10
2011	0	3	1	5	1	6	11	3.2	6	16
2012	0	0	0	4	1	7	16	3.3	10	14
2013	0	0	0	5	0	8	19	3.2	15	22
2014	0	0	0	6	0	9	19	3.0	18	24
2015	0	0	0	8	1	9	23	3.2	22	28

initiated was successful and produced two fledglings (male and female). The unpaired male present in 2007 occupied a territory adjacent to the breeding pair.

Seven of eight subadults released in fall 2007 were retained into the following breeding season (success rate = 0.87 vs. 0.37 in 2006). One female paired with the single male present in 2007, and four of the remaining subadults also paired to create three new PBGs. The 2008 breeding population consisted of 10 adults, including four PBGs, a helper male associated with the successful nesting pair in 2007, and a single male translocated in 2007.

Three successful nests in 2008 produced seven fledglings, but the nascent population crashed in August when tropical storm Fay passed over TTRS (Stewart and Beven 2009). TTRS received ~ 65 cm of rain during a 3-d period (J. Noble, unpubl. data), and surveys conducted afterwards revealed only eight surviving individuals. The survivors were distributed among five recruitment clusters, including three single males, the 2007 breeding pair and their offspring helper, and a male–female pair translocated in 2007.

Eleven subadults were translocated after tropical storm Fay (Table 2), but it took 2 yr for the population to return to the number present before the storm. Two females produced in TTRS in 2009 paired with the single males that survived Fay and nested successfully in 2010 (Table 2). A nestling female banded at Silver Lake Wildlife Management Area (30°48′N 84°42′W; Seminole County, Georgia) in 2008 dispersed a straight-line distance of 55 km, paired with a single male on TTRS, and nested successfully in 2010. An unmarked male was discovered in a previously unoccupied recruitment cluster in 2011. All translocated subadults and nestlings had been marked so the unmarked male was presumed to represent a second immigration event.

Although most subadults translocated after tropical storm Fay ($N = 11$; Table 2) remained on TTRS into the following breeding season, none successfully entered the breeding population. Failure to recruit into the breeding population coupled with aggressive interactions involving translocated subadults and established individuals led us to suspend translocations after the 2011 breeding season. At this point, six of the available recruitment clusters supported PBGs and the proportion of successful translocations had averaged 0.60 ± 0.21 (SD) annually (Table 2; excluding the small sample in 2008). Eight of 16 subadult males translocated to TTRS remained into the following breeding season and six successfully entered the breeding population. Eight of the 16 translocated subadult females also remained on TTRS into the following breeding season, but only four entered the breeding population.

Table 3. Non-parametric Mann–Whitney *U*-tests comparing features surrounding recruitment clusters that were occupied and used consistently (stable, $N = 8$) and clusters that were not occupied or were used and then abandoned (unstable, $N = 5$). A 300-m buffer was used to define the area surrounding each recruitment cluster. Values presented under stable and unstable clusters are means (SD) for the proportion of land cover and federal foraging criteria associated with different land-cover features.

Land cover/guidelines	U	P	Approx. χ^2	Stable clusters	Unstable clusters
Fields	29	0.19	1.7	0.09 (0.10)	0.04 (0.05)
Mesic hardwoods	17	0.66	0.2	0.05 (0.10)	0.07 (0.09)
Trail and roads	20	1.00	0	0.04 (0.01)	0.04 (0.02)
Upland pines	23	0.66	0.2	0.81 (0.13)	0.80 (0.08)
Wetlands	19	0.82	0.1	0.00 (0.01)	0.00 (0.01)
Federal guidelines <3	18	0.77	0.1	0.39 (0.09)	0.39 (0.05)
Federal guidelines 3–4	24	0.56	0.3	0.21 (0.11)	0.15 (0.14)
Federal guidelines >4	21	0.88	0.02	0.39 (0.11)	0.45 (0.19)

Population growth and reintroduction costs. Growth of the population averaged a new PBG annually after translocations were suspended (Table 2). In 2015, the adult population consisted of 18 breeders and nine helpers distributed among nine PBGs plus a territory held by a single, locally produced male. The 2015 breeding adults included 11 that had hatched at TTRS and assumed breeding positions, the immigrant female, and six birds translocated to TTRS as subadults. The translocated individuals present in 2015 represented 37.5% of all successfully translocated subadults (i.e., remained on TTRS into the next breeding season; $N = 16$) and most of the translocated individuals that entered the breeding population ($N = 10$).

Habitat conditions surrounding recruitment clusters did not influence cluster stability (Table 3). Upland pine forests dominated the area (>80%) within 300 m of all recruitment clusters, and approximately half of the pine forests surrounding recruitment clusters satisfied five or more federal foraging guidelines (Table 3). Recruitment clusters were initially occupied either by single males ($N = 6$) or pairs ($N = 4$). Initial occupancy by pairs was more common during the first 2 yr ($N = 3$). Nestling productivity on TTRS also was similar to the productivity observed elsewhere in the region ($t_{147} = -1.1$, $P = 0.28$). The number of nestlings per PBG averaged 2.2 ± 0.7 on TTRS compared to 2.0 ± 0.6 ($N = 128$) elsewhere in the Red Hills region.

During our reintroduction attempt, 154 artificial cavities were excavated (116 inserts and 40 advanced starts), and 47 artificial inserts were replaced as part of recurring cavity management. A natural cavity initiated in 2008 was completed and used as a nest cavity the following year (Table 4). Ten additional natural cavities were excavated, and six advanced starts were converted to completed cavities. In 2014, a single male was found using a natural cavity excavated >400 m from the nearest active cluster. The excavation of a natural cavity in an area far removed from other cavity trees was consistent with the pioneering behavior described for natural populations (USDI 2003).

DISCUSSION

There is no agreement on what a successful reintroduction entails (Shier 2015), but the progress of a reintroduction attempt can be assessed using the framework that Armstrong and Seddon (2008) proposed for addressing

Table 4. Milestones noted during the reintroduction of Red-cockaded Woodpeckers to Tall Timbers Research Station, 2006–2015. Translocations were suspended in 2011 when approximately half ($N = 6$) of the available breeding sites were occupied.

Milestone	Year
First successful nest	2007
First helper at nest	2008
First natural cavity completed	2009
First locally produced breeder	2010
First immigrant female	2010
First immigrant male	2011
Translocations suspended	2011
First locally produced breeding pair	2011
First pioneering event	2014

many of the questions associated with reintroduction biology. This framework includes a focus on (1) initial establishment, (2) growth and persistence though survival and local productivity, (3) meta-population interactions, and (4) ecosystem dynamics. This framework includes the period after translocations cease that has not been well documented for Red-cockaded Woodpeckers as well as consideration of the broader effects the reintroduction of this keystone species may have.

Initial establishment of Red-cockaded Woodpeckers on TTRS was achieved using fewer translocated individuals ($N = 27$) than used in the first reintroduction effort ($N = 40$; Hagan et al. 2004a). Our translocation success rate (0.62) was similar to rates reported elsewhere (0.42–0.82; Edwards and Costa 2004, Hagan et al. 2004a) and demonstrates that initial establishment can be achieved with ≤30 translocated subadults. Our large source population was capable of sustaining higher levels of removal (Hagan et al. 2004b), but minimizing the number of individuals taken from source populations could be an important consideration (Armstrong and Seddon 2008).

Growth of the population following initial establishment likely would have reached the goal of 10–12 PBGs by 2015 had tropical storm Fay not devastated the population in 2008. The threats tropical storms pose to Red-cockaded Woodpeckers have been linked primarily to the damage that high winds inflict on cavity trees (Engstrom and Evans 1990, Hooper and McAdie 1995), but heavy rains associated with tropical storms also appear to pose a threat. Losses associated with Fay were biased toward adult females (50% survived vs. 100% of adult males) and young of the year (none survived). We did not monitor evening roosting activity during Fay, but we did find one or more flooded cavities in each occupied recruitment cluster. In addition, losses attributable to Fay were not limited to TTRS. We banded 67 nestlings in 36 territories in the Red Hills region in 2008, but found only two subadults available for translocation after conducting 10 evening roost surveys in September (Table 2). A similar number of roost surveys typically documented ≥5 subadults in other years.

As our reintroduced population grew, retention and settlement patterns of translocated subadults were likely influenced by the habitat conditions and social environments that influence subadult dispersal decisions in natural populations (Kesler and Walters 2012). Habitat conditions defined by federal foraging guidelines varied subtly on TTRS (Fig. 1) and had no influence on cluster stability (Table 3). On the other hand, the social environment on TTRS changed markedly over time as locally produced young and immigrants helped the population grow. The presence of non-breeding helpers can lead to aggressive challenges to dispersing subadults (Kesler and Walters 2012), and this may explain the lack of recruitment by subadults translocated after Fay. Similar aggressive interactions have been reported where translocated subadults have been used to bolster small, isolated populations (<20 PBGs; S. McGee and M. Zondervan, pers. comm.).

The immigration of two Red-cockaded Woodpeckers into our reintroduced population suggests that the inter-population movements associated with meta-population dynamics were taking place. Even so, an important issue is whether the number of immigrants will be sufficient to offset the potentially negative effects of inbreeding in this small population. Inbreeding lowers productivity and juvenile survival of Red-cockaded Woodpeckers and is avoided if individuals interact with one another in natal territories (Daniels and Walters 2000). Our 2015 breeding population included six closely related breeding adults that hatched in different years and lacked such familiarity (as well as the parents of these individuals). We have not yet had any breeding pairs comprised of closely related individuals (based on pedigree), but the founding population was small (12 individuals including the two immigrants) and will likely encounter high levels of inbreeding ($F \geq 0.15$ based on Soule and Wilcox 1980) within 3–4 generations (~ 15–20 yr) in the absence of continued and frequent immigration (Haig et al. 1993).

Wallace and Buchholz (2001) found that breeding adults readily accepted nestlings translocated from other nests. Translocating nestlings could be an alternative strategy for introducing novel genotypes to TTRS given the effect the current social environment (seven territories with helpers) may have on the retention of translocated subadults. Haig et al. (1993) noted that nestlings also could be cross-fostered more strategically than subadults by focusing efforts on breeding pairs with high kinship values. Same-aged nestlings could be transported to TTRS from other woodpecker territories in the Red Hills in less than an hour and at reduced costs compared to translocation of subadults.

The ecosystem functions associated with reintroduction attempts will likely arise through the role that Red-cockaded Woodpeckers play as a keystone cavity excavator (Blanc and Walters 2008a). The many artificial cavities we provided coupled with frequent replacement of older unused artificial cavities likely enhanced population stability and growth while also providing roost and nest sites for many organisms (including cavity competitors). However, cavity-nesting species such as Northern Flickers (*Colaptes auratus*) preferentially use abandoned, enlarged cavities excavated by Red-cockaded Woodpeckers rather than inserts (Blanc and Walters 2008b). Continued excavation of natural cavities and advanced starts by our reintroduced population should eventually enhance numbers of Northern Flickers and other cavity-nesting birds on TTRS.

The cost of our reintroduction effort was ~ \$211,000 during the first 5 yr. The field equipment needed (e.g., ladders, video peepers, banding equipment, chainsaw, and drill) added an additional \$6700 to estimated expenses. Current management efforts cost an average of \$6500 annually and focus on monitoring the population and performing cavity maintenance (but that does not include the costs of prescribed burns used to maintain habitat). Annual expenses will likely increase by <10% if efforts to introduce new genetic stock are initiated using cross-fostered nestlings, but the reintroduction effort has progressed well and provided new information on the reintroduction process for this imperiled species (Table 4). The reestablished population also has helped to satisfy Florida's management goals for the Red Hills region (FFWCC 2003) and created an opportunity to test methods for enhancing the persistence of a small Red-cockaded Woodpecker population, a trait shared with other populations where reintroduction is being considered (O'Gara et al. 2015). The reintroduction effort has also provided valuable educational opportunities through the outreach efforts conducted on TTRS ($N = 951$ participants in 2015 that included professional land managers, university classes, scientific organizations, and the general public).

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LITERATURE CITED

ALLEN, D. H. 1991. Constructing artificial Red-cockaded Woodpecker cavities. USDA Forest Service General Technical Report SE 73, Ashville, NC.

ARMSTRONG, D. P., AND P. J. SEDDON. 2008. Directions in reintroduction biology. Trends in Ecology and Evolution 23: 20–25.

BAKER, W. W. 1983. Decline and extirpation of a population of Red-cockaded Woodpeckers in northwest Florida. In: Red-cockaded Woodpecker Symposium II (D. A. Wood, ed.), pp. 44–45. Florida Game and Fresh Water Fish Commission, Tallahassee, FL.

BLANC, L. A., AND J. R. WALTERS. 2008a. Cavity-nest webs in a longleaf pine ecosystem. Condor 110: 80–92.

———, AND ———. 2008b. Cavity excavation and enlargement as mechanisms for indirect interactions in an avian community. Ecology 89: 506–514.

CARRIE, N. R., R. N. CONNER, D. C. RUDOLPH, AND D. K. CARRIE. 1999. Reintroduction and post-release movements of Red-cockaded Woodpecker groups in eastern Texas. Journal of Wildlife Management 63: 824–832.

COPEYON, C. K. 1990. A technique for constructing cavities for the Red-cockaded Woodpecker. Wildlife Society Bulletin 18: 303–311.

COSTA, R., AND R. S. DELOTELLE. 2006. Reintroduction of fauna to longleaf pine ecosystems. In: The longleaf pine ecosystem: ecology, silviculture, and restoration (S. Jose, E. J. Jokela, and D. L. Miller, eds.), pp. 335–376. Springer, New York, NY.

COX, J. A., W. W. BAKER, AND R. T. ENGSTROM. 2001. Red-cockaded Woodpeckers in the Red Hills region: a GIS-based assessment. Wildlife Society Bulletin 29: 1278–1288.

CRAWFORD, R. L. 1978. Autumn bird casualties at a northwest Florida TV tower: 1973–1975. Wilson Bulletin 90: 335–345.

———, W. R. BRUECKHEIMER, AND W. W. ROGERS. 2012. The legacy of a Red Hills hunting plantation: Tall Timbers Research Station and Land Conservancy. University Press of Florida, Gainesville, FL.

DANIELS, S. J., AND J. R. WALTERS. 2000. Inbreeding depression and its effects on natal dispersal in Red-cockaded Woodpeckers. Condor 102: 482–491.

DEFAZIO, J. T., Jr., M. A. HUNNICUTT, M. R. LENNARTZ, G. L. CHAPMAN, AND J. A. JACKSON. 1987. Red-cockaded Woodpecker translocation experiments in South Carolina. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 41: 311–317.

EDWARDS, J. W., AND R. COSTA. 2004. Range-wide success of Red-cockaded Woodpecker translocations. In: Red-cockaded Woodpecker: road to recovery (R. Costa and S. J. Daniels, eds.), pp. 307–311. Hancock House Publishers, Blain, WA.

ENGSTROM, R. T., R. L. CRAWFORD, AND W. W. BAKER. 1984. Breeding bird populations in relation to changing forest structure following fire exclusion: a 15-year study. Wilson Bulletin 96: 437–450.

———, AND G. W. EVANS. 1990. Hurricane damage to Red-cockaded Woodpecker (*Picoides borealis*) cavity trees. Auk 107: 608–610.

ESRI. 2006. ArcGIS 3.2. Environmental Systems Research, Redlands, CA.

FLORIDA FISH AND WILDLIFE CONSERVATION COMMISSION (FFWCC) [ONLINE]. 2003. Management plan for the Red-cockaded Woodpecker (*Picoides borealis*). FFWCC, Tallahassee, FL. <www.myfwc.com/media/1355359/RCW_management_plan.pdf> (Accessed 16 August 2016).

GARABEDIAN, J. E., C. E. MOORMAN, M. N. PETERSON, AND J. C. KILGO. 2014. Systematic review of the influence of foraging habitat on Red-cockaded Woodpecker reproductive success. Wildlife Biology 20: 37–46.

GRIFFITH, B., J. M. SCOTT, J. W. CARPENTER, AND C. REED. 1989. Translocation as a species conservation tool: status and strategy. Science 245: 477–480.

HAGAN, G., R. COSTA, AND M. PHILLIPS. 2004a. Reintroduction of the first Red-cockaded Woodpeckers into unoccupied habitat: a private land and conservation success story. In: Red-cockaded Woodpecker: road to recovery (R. Costa and S. J. Daniels, eds.), pp. 341–346. Hancock House Publishers, Blain, WA.

———, R. T. ENGSTROM, J. A. COX, AND P. SPIVEY. 2004b. Effects of translocation on a large Red-cockaded Woodpecker population. In: Red-cockaded Woodpecker: road to recovery (R. Costa and S. J. Daniels, eds.), pp. 320–324. Hancock House Publishers, Blain, WA.

HAIG, S. M., J. R. BELTHOFF, AND D. H. ALLEN. 1993. Population viability analysis for a small population of Red-cockaded Woodpeckers and an evaluation of enhancement strategies. Conservation Biology 7: 289–301.

HOOPER, R. G., AND C. J. MCADIE. 1995. Hurricanes and the long-term management of the Red-cockaded Woodpecker. In: Red-cockaded Wood pecker: recovery, ecology, and management (D. L. Kulhavy, R. G. Hooper, and R. Costa, eds.), pp. 148–166. Center for Applied Studies in Forestry, Stephen F. Austin State University, Nacogdoches, TX.

JACKSON, J. A. 1994. Red-cockaded Woodpecker (*Picoides borealis*). In: The birds of North America online (A. Poole, ed.). Cornell Lab of Ornithology, Ithaca, NY.

KESLER, D. C., AND J. R. WALTERS. 2012. Social composition of destination territories and matrix habitat affect Red-cockaded Woodpecker dispersal. Journal of Wildlife Management 76: 1028–1035.

LAMMERTINK, M. 2014. Trends in threat status and priorities in conservation of the woodpeckers of the world. Acta Ornithologica 49: 207–219.

LIGON, J. D., P. B. STACEY, R. N. CONNER, C. E. BOCK, AND C. S. ADKISSON. 1986. Report of the American Ornithologists' Union Committee for the conservation of the Red-cockaded Woodpecker. Auk 103: 848–855.

O'GARA, K., J. MILES, AND R. MAY. 2015. Feasibility of Red-cockaded Woodpecker (*Picoides borealis*) reintroduction into the pine flatwoods communities of Jonathan Dickinson State Park, Florida. Florida Field Naturalist 43: 47–104.

PASINELLI, G., AND J. R. WALTERS. 2002. Social and environmental factors affect natal dispersal and philopatry of male Red-cockaded Woodpeckers. Ecology 83: 2229–2239.

RUDOLPH, D. C., R. N. CONNER, AND J. R. WALTERS. 2004. Red-cockaded Woodpecker recovery: an integrated strategy. In: Red-cockaded Wood pecker: road to recovery (R. Costa and S. J. Daniels, eds.), pp. 70–76. Hancock House Publishers, Blain, WA.

SHIER, D. M. 2015. Developing a standard for evaluating reintroduction success using IUCN Red List indices. Animal Conservation 18: 411–412.

SOULE, M. E., AND B. A. WILCOX. 1980. Conservation biology: an evolutionary-ecological perspective. Sinauer Associates, Sunderland, MA.

STEWART, S. R., AND J. L. BEVEN II. 2009. Tropical cyclone report tropical storm Fay (AL062008) 15–26 August 2008. National Hurricane Center, Miami, FL.

SUTHERLAND, W. J., D. ARMSTRONG, S. H. BUTCHART, J. M. EARNHARDT, J. EWEN, I. JAMIESON, C. G. JONES, R. LEE, P. NEWBERY, J. D. NICHOLS, K. A. PARKER, F. SARRAZIN, P. J. SEDDON, N. SHAH, AND V. TATAYAH. 2010. Standards for documenting and monitoring bird reintroduction projects. Conservation Letters 3: 229–235.

SYSTAT. 2007. Systat for Windows (version 12.0). Systat Software Inc., San Jose, CA.

U. S. DEPARTMENT OF INTERIOR (USDI). 2003. Red-cockaded Woodpecker recovery plan. USDI, Fish and Wildlife Service, Southeastern Region, Atlanta, GA.

WALLACE, M. T., AND R. BUCHHOLZ. 2001. Translocation of Red-cockaded Woodpeckers by reciprocal fostering of nestlings. Journal of Wildlife Management 65: 327–333.

WALTERS, J. R., C. K. COPEYON, AND J. CARTER III. 1992. Test of the ecological basis of cooperative breeding in Red-cockaded Woodpeckers. Auk 109: 90–97.

———, L. B. CROWDER, AND J. A. PRIDDY. 2002. Population viability analysis for Red-cockaded Woodpeckers using an individual-based model. Ecological Applications 12: 249–260.

———, P. D. DOERR, AND J. CARTER. 1988. The cooperative breeding system of the Red-cockaded Woodpecker. Ethology 78: 275–305.