Original Research Article

Using qualitative methods to support recovery of endangered species: The case of red-cockaded woodpecker foraging habitat

James E. Garabedian [a, *], M. Nils Peterson [a], Christopher E. Moorman [a], John C. Kilgo [b]

[a] Fisheries, Wildlife, and Conservation Biology Program, North Carolina State University, Raleigh, NC, USA
[b] USDA Forest Service Southern Research Station, New Ellenton, SC, USA

A B S T R A C T

Meta-analyses are powerful tools for synthesizing wildlife-habitat relationships, but small sample sizes and complex species-habitat relationships often preclude correlative meta-analyses on endangered species. In this study, we demonstrate qualitative comparative analysis (QCA) as a tool that can reliably synthesize habitat-fitness relationships from small sample sizes for species with narrow habitat requirements. We apply QCA to results from a habitat threshold regression tree model and identify habitat thresholds with consistent positive effects on fitness of the federally endangered red-cockaded woodpecker (*Dryobates borealis*; RCW) on the Savannah River Site, USA. We reformulated regression tree results in a QCA framework to examine the consistency of threshold effects on RCW fledgling production at the individual group level ($n = 47$). Synthesizing regression tree results with QCA revealed alternative combinations of habitat thresholds that in conjunction with group size consistently led to above-average fledgling production for 41 of 47 (88%) individual RCW groups. Importantly, QCA identified unique combinations of habitat thresholds and group size related to above-average fledgling production that were not retained in the regression tree model due to small sample sizes. Synthesizing a small habitat-fitness dataset using QCA provided a tractable method to identify unique combinations of habitat and group size conditions that are consistently important to individual fitness, but may not be detected by meta-analyses that can be biased by small sample sizes. QCA offers a viable approach for synthesis of habitat-fitness relationships and can be extended to address many complex issues in endangered species recovery when correlative meta-analyses are not possible.

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1. Introduction

Conservation professionals need reliable evidence on the degree to which management strategies are successful in achieving conservation objectives (Pullin and Knight, 2001). Meta-analyses can provide reliable quantitative evidence by identifying management strategies that consistently help achieve conservation objectives. Meta-analytic studies leverage

data from multiple primary studies to provide greater insight on which habitat management strategies have consistent effects on populations of threatened and endangered species (Stewart, 2010), thereby increasing the likelihood for species' recovery (Vetter et al., 2013). Meta-analyses provide a significant benefit to synthesis of quantitative evidence by increasing statistical power and precision of estimated effects of management strategies (Nakagawa and Santos, 2012).

The paucity of datasets describing effects of different habitat management strategies on endangered species, however, often precludes use of correlative meta-analyses to support conservation decisions. It is difficult to obtain an adequate sample size to conduct formal meta-analyses of management strategies due to practical challenges in collection of species-habitat data (Beaudry et al., 2010), under-reporting of non-significant results (Koricheva, 2003), and disparate site-histories (Tempel et al., 2016). Quantitative estimates of habitat management effects are limited for many conservation reliant species (Boarman and Kristan, 2006; Schultz et al., 2008). Moreover, datasets on effects of management strategies on endangered species may only include measurements on a small number of focal individuals in a population, thereby failing to satisfy assumptions of parametric modeling techniques (Koricheva and Gurevitch, 2014), and preventing controlled comparisons among focal individuals or groups (Carrete et al., 2008). Such data limitations may hinder identification of consistent success or failure of particular management strategies (Dixon-Woods et al., 2005). Even flexible habitat modeling techniques, such as regression trees, may not detect consistent effects of habitat management when data is limited to a small number of focal individuals (Elith et al., 2008; Vaughan and Ormerod, 2005). The consequence is that support for recovery of endangered and threatened species may be restricted to limited data from a single or small set of habitat studies that are not amenable to formal quantitative meta-analyses (Nakagawa and Santos, 2012). Collectively, these challenges highlight the need to make more efficient use of all available data and modeling strategies in support of conservation decisions (Brigham et al., 2002; Schaub et al., 2007).

Case-oriented qualitative methods can utilize limited data to facilitate inference based on consistency of successes or failures of management strategies when quantitative meta-analytic techniques are not possible. Case-oriented methods emphasize the consistency of outcomes based on conditions of individual cases, recognizing that quantitative generalization of effect sizes is one of many approaches to characterize species' responses to management strategies (Byrne and Ragin, 2009). Qualitative comparative analysis (QCA; Ragin, 1987), for example, employs Boolean algebra to make inferences on what conditions, or combinations of conditions, consistently lead to a specific outcome across individual cases (Thiem, 2016). One advantage of QCA is the ability to analyze complex interactions among conditions without stringent data requirements of parametric models (Rudel, 2008). Additionally, QCA is a suitable technique for analysis of a small number of cases, and thus can complement variable-oriented regression models that may be biased by small sample sizes (Magliocca et al., 2015). Case-oriented methods like QCA have been applied in social sciences for several decades to identify the combination(s) of conditions (i.e., pathways) that lead to a specific outcome (Rihoux and Ragin, 2009). However, the use of these methods to support wildlife conservation has been limited (but see Rudd, 2015).

In this study, we demonstrate QCA as a tool that can synthesize limited data and provide reliable evidence about habitat threshold-fitness relationships to support conservation of the federally endangered red-cockaded woodpecker (*Dryobates borealis*; RCW). RCWs represent a case in which a small set of primary correlative habitat-fitness studies provided quantitative support for range-wide foraging habitat thresholds (U.S. Fish and Wildlife Service [USFWS], 2003). Quantitative techniques typically used to synthesize habitat-fitness relationships have not been applied all to RCWs due to a limited number of primary studies and small sample sizes (Garabedian et al., 2014b). Additionally, primary studies have shown RCW habitat-fitness relationships are driven by interactions among several foraging habitat features and group size (James et al., 2001, 1997), which may bias correlations in small datasets. Consequently, uncertainty persists regarding which foraging habitat thresholds, or combinations thereof, consistently lead to improvements in fitness of individual RCW groups (Garabedian et al., 2014b). Thus, case-oriented qualitative methods such as QCA that overcome issues related to insufficient data and modeling complex interactions have potential to address inconsistencies in RCW foraging habitat-fitness relationships.

The RCW is a cooperative breeder associated with mature, fire-maintained pine (*Pinus* spp.) forests of the southern USA (Conner et al., 2001). RCWs live in social groups consisting of a breeding pair and up to 4 helpers, plus the current year's fledglings (Ligon, 1970). Almost all females disperse following fledging, whereas nearly all male fledglings stay as helpers or disperse to fill breeding vacancies in neighboring clusters (Walters, 1990; Walters et al., 1992). Larger groups typically have higher reproductive success and improved breeder survival due to the presence of helpers (Lennartz et al., 1987; Khan and Walters, 2002). Groups also have greater reproductive success in areas with low to moderate pine density and large and old pines (e.g., $\geq$ 35.6 cm dbh and > 60 years old) for foraging and cavity excavation (James et al., 1997, 2001; Walters et al., 2002). Cavity trees have been identified as the critical limiting resource for RCWs (Walters et al., 1992), in part because natural cavities can take several years to excavate (Conner and Rudolph, 1995). Habitat loss, particularly large and old longleaf pines (*P. palustris*) used for nesting and roosting, was the primary historic cause of the species' decline (Walters, 1991). The effects of habitat loss (Conner and O'Halloran, 1987; Conner and Rudolph, 1991; Rudolph and Conner, 1991) and fire suppression (Conner et al., 2006; Conner and Rudolph, 1989; Costa and Escano, 1989) have been well studied in the context of nesting habitat (i.e., the cavity tree cluster and area within approximately 61 m of the cluster), which has been the foremost limiting factor for RCW recovery (Walters et al., 1992). Accordingly, recovery strategies have emphasized installation of recruitment clusters (i.e., aggregates of artificial cavities installed in unoccupied RCW habitat; USFWS, 2003) as a means to rapidly stabilize and increase RCW populations (Copeyon et al., 1991).

As nesting habitat limitations are being mitigated through intensive management of existing RCW cavity trees, prescribed fire, and installation of artificial cavities, provision of foraging habitat has become an essential component of the species' recovery (Walters et al., 2002). RCW group fitness increases with provision of open foraging habitat with low to intermediate pine densities, some large and old pines, intermittent midstory trees and shrubs, and abundant herbaceous groundcover (James et al., 2001, 1997; Walters et al., 2002). Accordingly, foraging habitat thresholds were developed to provide foraging habitat management targets for: 1) substantial herbaceous groundcover, 2) minimal hardwood midstory, 3) minimal pine midstory, 4) minimal hardwood overstory, 5) low to intermediate density of small and medium pines, and 6) a significant presence of large and old pines (USFWS, 2003).

Recent studies of RCW resource selection and fitness suggest that satisfying the entire set of habitat threshold criteria is neither realistic (Hiers et al., 2016) nor required to recover RCW populations (Garabedian et al., 2014a). Many RCW populations are healthy and growing on sites where foraging habitat does not satisfy current USFWS foraging habitat guidelines (McKellar et al., 2014). Determining how RCW populations are growing in areas with inadequate foraging habitat has proven difficult due to practical challenges in collecting sufficient data to develop correlative models. Datasets on RCW habitat threshold-fitness relationships typically are limited (e.g., 30 individual RCW groups) because sample sizes are determined by the number of potential breeding groups (i.e., a breeding pair plus 0—5 helper individuals), not the total number of individuals in a population (USFWS, 2003). Home-range data are recommended for delineating foraging habitat to individual groups; however, collection of these data is resource intensive, and rarely used as a result (USFWS, 2003). Moreover, data on foraging habitat thresholds requires measurement of fine-grained forest structure throughout RCWs' home ranges (Garabedian et al., 2014a, 2017). As a consequence, it has been challenging to establish consistent relationships between provision of RCW foraging habitat thresholds and group reproductive success using site-specific correlative models (e.g., multiple linear regression; Spadgenske et al., 2005; Butler and Tappe, 2008; Garabedian et al., 2017). Few published correlative RCW habitat-fitness models account for > 30% of variation in group reproductive success, and individual coefficient estimates typically range from −0.100 to 0.100, suggesting individual foraging habitat components have relatively small effects on group fitness (Garabedian et al., 2014b).

The inconsistent relationships between the USFWS recovery plan foraging habitat thresholds and RCW reproductive success suggests: 1) the effects of individual foraging habitat thresholds on RCW reproductive success are contingent on the presence or absence of other foraging habitat thresholds (James et al., 2001, 1997) or group size (Garabedian et al., 2017); or 2) there are combinations of habitat threshold conditions that can lead to above-average reproductive success for individual groups not captured by correlative models. Therefore, using QCA to synthesize site-specific habitat threshold-fitness relationships at the level of individual groups may provide more robust decision support for RCW conservation. Our goal was to demonstrate how QCA can be used to synthesize limited data and reduce uncertainty with a case study of RCW habitat threshold-fitness relationships on the Savannah River Site (SRS), South Carolina. Specifically, our objective was to determine if habitat threshold-fitness relationships obtained from a site-specific regression tree model are consistent among individual RCW groups on SRS. Site-specific RCW habitat threshold-fitness relationships often deviate from current range-wide foraging habitat guidelines, representing a challenge to ongoing management (McKellar et al., 2014). Therefore, we designed a case study to represent a scenario in which decision support for endangered species conservation is constrained to habitat thresholds obtained from a limited site-specific quantitative dataset.

2. Methods

2.1. Savannah River Site RCW population

The SRS is an 80,267-ha National Environmental Research Park owned and operated by the U.S. Department of Energy. Located on the Upper Coastal Plain and Sandhills physiographic provinces in South Carolina, USA, the SRS is characterized by sandy soils and gently sloping hills dominated by pines with scattered hardwoods (Kilgo and Blake, 2005). Prior to federal acquisition in 1951, the majority of the SRS was maintained in agricultural fields or recently had been harvested for timber (White, 2005). The U.S. Department of Agriculture Forest Service managed the natural resources on the SRS since 1952 and reforested the majority of the site (Imm and McLeod, 2005). Approximately 53,014 ha of the SRS was re-forested with artificially regenerated stands of loblolly (*P. taeda*), longleaf, and slash (*P. elliottii*) pines with an additional 2832 ha with pine-hardwood mixtures. Mixed pine-hardwood stands on SRS typically include a mixture of longleaf pine, loblolly pine, and *Quercus* spp. Midstory trees that reach the subcanopy typically are small *Quercus* spp., but midstory hardwoods also include hickories (*Carya* spp.), sweetgum (*Liquidambar styraciflua*), and sassafras (*Sassafras albidum*). The remaining ~27,000 ha of forested area on the SRS includes bottomland hardwoods, forested wetlands/riparian areas, and mixed-hardwood stands.

In conjunction with the Department of Energy, the Forest Service began management and research on the RCW in 1984 with the objective to restore a viable population on SRS. Under intensive management since 1985, the RCW population has grown from 3 groups of 4 birds (Johnston, 2005) to 98 groups with more than 250 birds in 2018 (T. Mims, *pers. comm.*). The rapid growth of the SRS RCW population has occurred during a period of time when < 20% of RCW habitat on SRS satisfies all USFWS recovery thresholds (Garabedian et al., 2014a, Table 1). The SRS RCW population is designated as a secondary core

Table 1
Habitat thresholds listed in the U.S. Fish and Wildlife Service (USFWS, 2003) red-cockaded woodpecker recovery plan.

Foraging habitat attribute	USFWS recovery threshold
Herbaceous groundcover	$\geq 40\%$
Hardwood midstory	sparse and < 2.1 m in height
Pines ≥ 35.6 cm dbh	BA ≥ 4.6 m^2/ha and ≥ 45 stems/ha
Pines 25.4−35.6 cm dbh	BA < 9.2 m^2/ha
Pines ≥ 25.4 cm dbh	BA ≥ 2.3 m^2/ha
Pines < 25.4 cm dbh	BA < 2.3 and < 50 stems/ha
Hardwood canopy cover	$< 30\%$ cover

population in the South Atlantic Coastal Plain recovery unit and must support > 250 potential breeding groups (i.e., a male and female occupying the same cluster of cavity trees) at the time of and after delisting (USFWS, 2003).

2.2. Data acquisition

2.2.1. Home-range data

We used home-range data collected for RCW groups ($n = 47$) on SRS to delineate habitat available to individual groups (Garabedian et al., 2018a). We visually tracked RCW groups for 4−8 h (hereafter, home-range follows), twice a month between March 2013 and April 2015. Following Franzreb (2006), we used handheld GPS to record RCW locations at 15-min intervals. Minimally, we obtained 15 location fixes throughout the day during each follow, thus providing ≥ 30 relocations per month. Follows consisted of sustained visual contact with individuals of the sample group beginning when individuals left their roosts in the morning and continuing until contact with the birds was lost, or until terminated due to inclement weather or management activities that precluded site access (e.g., prescribed burning). Although RCW group members tend to forage near one another, even concurrently in the same tree (Franzreb, 2006), we used location fixes for the breeding male of each sample group to represent movement of the entire group.

2.2.2. Foraging habitat structure

Following Garabedian et al. (2014a), we used LiDAR-derived estimates for density and BA (m^2/ha) of pines ≥ 35.6 cm dbh, pines 25.4−35.6 cm dbh, pines < 25.4 cm dbh, and hardwoods 7.6−22.9 cm dbh, and percent hardwood canopy cover to characterize foraging habitat available to individual RCW groups. Garabedian et al. (2014a) used regression methods to relate the LiDAR sensor data to forest inventory measurements collected across a range of forest conditions on the SRS. They used the resulting regressions to predict forest structural attributes included in the RCW recovery plan (USFWS, 2003) and generate raster layers at 20-m resolution across the entire SRS. An 80-m grain size was optimal for characterizing foraging habitat quality based on their objective to minimize prediction error and maintain a grain size concordant with recommended spatial scale for assessment and management of RCW foraging habitat (Garabedian et al., 2014a). We used the Zonal toolset in the Spatial Analyst toolbox in ArcGIS to extract mean values for LiDAR-derived habitat attributes within each RCW home range (ESRI, 2017).

2.2.3. Group productivity

As part of ongoing monitoring, the Forest Service conducted RCW group observations and nest checks during each nesting season since 1985 to determine clutch size, nestling production, fledgling production, and group size for each cluster. We used fledgling production and group size for each of the 47 sample groups during 2013 and 2014 in subsequent analyses.

3. Data analysis

We demonstrate how QCA can synthesize evidence obtained from a site-specific regression tree model to provide detailed insight about the consistency of habitat threshold effects on fitness at the individual RCW group-level. Specifically, we used the full regression tree results to define the case-level (i.e., group-level) binary conditions and outcomes and subsequently apply crisp-set QCA to the reformulated dataset.

3.1. Qualitative comparative analysis

QCA is based in set theory and the premise that a particular outcome can occur under alternative combinations of certain conditions (Ragin, 1987). Essentially, QCA organizes individual cases into different "sets" that exhibit similar combinations of conditions and outcomes, and then uses Boolean algebra to identify the conditions that consistently lead to the outcome of interest (Ragin, 1999). A "crisp-set" QCA examines combinations of binary conditions and their relationships with a binary outcome (Rihoux and Ragin, 2009). The technique is designed specifically for a small to moderate number of cases, and

provides a favorable alternative to correlative methods (e.g., logistic regression) when analyzing small datasets and binary indicators of habitat quality (Dell'Angelo et al., 2017). QCA places emphasis on the logical relationships between combinations of conditions and a specific outcome, rather than average effect sizes. The emphasis on logical relationships retains alternative and potentially unique combinations of conditions that may not be detected in correlative models (Oldekop et al., 2010; Rudel, 2008).

The conditions retained by QCA are interpreted as either necessary or sufficient. A condition is necessary if it is present in all cases exhibiting the outcome of interest, but does not produce the outcome of interest when considered in isolation of other conditions. For example, a breeding pair is necessary for sexual reproduction, but in isolation the presence of a breeding pair does not guarantee reproductive success. A condition is sufficient if the outcome occurs whenever the condition is present in conjunction with other conditions. Sufficient conditions are central to QCA because they represent alternative pathways to the same outcome (Ragin, 1987). For example, the presence of adequate food resources in conjunction with a breeding pair can be sufficient for above-average reproductive success (Schneider and Wagemann, 2012). Similarly, the absence of intraspecific competition in conjunction with a breeding pair can be sufficient for above-average reproductive success. The Quine-McCluskey algorithm (McCluskey, 1956) is used to reduce all possible combinations of necessary and/or sufficient conditions into a parsimonious solution. Parsimonious solutions include only non-redundant combinations of conditions that lead to the outcome of interest. For example, the presence of adequate food resources or absence of intra-specific competition in conjunction with a breeding pair may represent alternative and non-redundant combinations of conditions (i.e., pathways) that lead to above-average reproductive success.

In QCA, consistency and coverage are metrics that describe goodness of fit of necessary and sufficient conditions, and the parsimonious solution (Ragin, 2006). Consistency describes how often a given condition (or combination of conditions) occurs with a given outcome, and resembles statistical significance in parametric models (Legewie, 2013; Thiem, 2010). Coverage measures the empirical relevance of a given condition (or combination) and indicates the extent to which a given condition (or combination) is the only observed path to the outcome of interest (Thomas et al., 2014). Coverage roughly corresponds to partitioned variance (R^2) in a regression model (Ragin, 2006). Consistency and coverage values range from 0 to 1, with 0 indicating no consistency (or coverage) and 1 indicating perfect consistency (or coverage). For example, if the threshold of ≥ 45 pines ≥ 35.6 cm dbh/ha was identified as a necessary condition for above-average reproductive success for 18 of 20 RCW groups, the consistency score for the threshold would be 18/20, or 0.9. Combinations of conditions with consistency and coverage values ≥ 0.9 and ≥ 0.5, respectively (Ragin, 2006), are retained in a parsimonious solution. The conditions retained in a parsimonious solution cannot be dropped without reducing consistency and coverage below the acceptable values (Ragin et al., 2003).

3.2. Regression tree habitat thresholds

Regression trees are flexible models that use recursive binary splitting to identify thresholds of predictor variables that partition species' responses into two mutually exclusive, homogeneous groups (Breiman et al., 1984). Split values (i.e., thresholds) for predictor variables are determined by rules that minimize residual variance within each of the two groups. Splitting begins with a single predictor variable at the top of the tree and continues until data are not sufficient for further splits or no additional splits are supported by the data. Recursive splitting in regression trees induces a natural hierarchy in model output such that the average species' response in a lower split depends on higher splits in the tree, so higher-order interactions among predictors are automatically modeled (Elith et al., 2008). Because of the hierarchical nature of regression trees, lower splits are based on fewer samples than the initial ones, and thus tend to have low predictive power. Pruning is the process of reducing a full regression tree to the optimal size by eliminating lower splits with too few samples or high levels of within-group residual variance.

We developed regression trees to identify habitat thresholds that lead to above-average reproductive success for RCWs ($n = 47$) on SRS. We fit regression trees with fledgling production as the response variable, and mean values of LiDAR-derived habitat attributes within RCW home ranges and group size as predictors. We included group size because larger RCW groups tend to have higher fledgling production (Khan and Walters, 2002; Walters, 1990). We selected the final trees with the smallest error rate using 50 sets of 10-fold cross validations and the 1-SE rule (De'ath and Fabricius, 2000). We conducted the regression tree analysis in the R statistical environment (R Development Core Team, 2015) using the contributed package "rpart" (Therneau et al., 2015).

3.3. Applying QCA to regression tree results

We reformulated the SRS full regression tree thresholds in a crisp-set QCA framework to examine the consistency of regression tree threshold effects on RCW fledgling production at the individual-group level. We treated each of the 47 RCW groups in the regression tree dataset as individual cases. For each case, we defined the conditions using measures of foraging habitat structure within home ranges and the outcomes using fledgling production (i.e., a truth table; Table 2). If the mean habitat conditions within the home range of a given group satisfied a threshold condition identified in regression trees, we coded the habitat threshold condition as present (1); if mean conditions did not satisfy threshold conditions, we coded the habitat threshold condition as absent (0; Table 2). For example, if the SRS regression tree indicated groups with ≥ 45 pines $\geq$ 35.6 cm dbh/ha within their home range have above average fitness, then we coded the habitat threshold condition as present

Table 2

Truth table for regression tree output with presence or absence of habitat thresholds within individual red-cockaded woodpecker (RCW) group home-ranges and group size as the conditions (Conditions) and the associated effect on RCW group fledgling production as the outcome (Outcome). Following QCA and Boolean logic convention, conditions present within home ranges are coded as 1 and those absent are coded as 0. Group size conditions are coded 1 for groups of ≥ 3 individuals and 0 for groups of <3 individuals. Fledgling production is coded 1 for groups with fledgling production ≥ 1.6 (the average fledgling production for all 47 groups) and 0 if they did not.

n cases	Conditions				Outcome	Raw consistency
	Group size	HWMID	BA PINES ≥ 35	BA PINES 25-35	Fledge prod	
2	1	0	1	0	1	1
2	1	1	0	0	1	1
1	0	0	0	1	1	1
1	1	0	1	1	1	1
1	1	1	0	1	1	1
1	1	1	1	1	1	1
6	0	0	1	1	1	0.833
12	0	1	1	0	1	0.752
7	0	1	1	1	0	0.286
13	0	1	0	0	0	0.231
1	0	1	0	1	0	0

[a] BA PINES ≥ 35 = basal area (m²/ha) of pines ≥ 35 cm dbh; BA PINES $25-35$ = basal area of pines $25-35$ cm dbh; HWMID = basal area of hardwood midstory trees $7.6-22.9$ cm dbh; Group Size = the total number of individuals in the group. Threshold conditions for group size were present if group sizes were > 3, threshold conditions for hardwood midstory were present if BA was < 0.97 m²/ha, threshold conditions for pines ≥ 35 cm dbh were present if basal area was ≥ 5.1 m²/ha, and threshold conditions for pines $25-35$ cm dbh were present if BA was ≥ 10 m²/ha.

(1) for all RCW groups that had home-ranges with on average ≥ 45 pines ≥ 35.6 cm dbh/ha, and absent (0) if < 45 pines ≥ 35.6 cm dbh/ha. If individual group sizes were larger than the threshold for group size identified in regression trees, we coded the group size threshold as present (1); if group sizes were smaller, we coded the threshold for group size as absent (0; Table 2). Likewise, we used fledgling production of each group to define the outcomes associated with the habitat conditions within home ranges. If fledgling production of a group was above the average for the entire sample (≥ 1.6 fledglings), we coded the outcome as present (1); if fledgling production was below average, the outcome was absent (0; Table 2). Alternatively, without site-specific quantitative data, habitat thresholds could be defined using established relationships from other areas or information contained in the species' recovery plan.

We report the necessary and sufficient conditions, and the parsimonious solution(s) that consistently lead to above-average group reproductive success. Following Thiem et al. (2018), we used 0.9 and 0.5 as minimum values for consistency and coverage, respectively. We conducted the QCA analysis in the R statistical environment using the contributed package "QCApro" (Thiem et al., 2018).

4. Results

4.1. Regression tree results used for QCA

The full regression tree identified thresholds for group size, BA of hardwoods $7.6-22.9$ cm dbh, BA pines ≥ 35.6 cm dbh, and BA pines $25.4-35.6$ cm dbh that predicted significant changes in average fledgling production (1.6 fledglings produced; Fig. 1). Group size was most important to average fledgling production, where groups with ≥ 3.5 individuals on average had the highest fledgling production. BA of hardwoods $7.6-22.9$ cm dbh was second most important, where ≥ 0.97 m²/ha BA reduced average fledgling production. BA of pines ≥ 35.6 cm dbh was third most important to average fledgling production, where < 5.1 m²/ha BA predicted lower average fledgling production. Finally, BA of pines $25.4-35.6$ cm dbh was fourth most important to average fledgling production, where BA ≥ 10 m²/ha predicted the lowest average fledgling production in the sample.

The pruned regression tree retained thresholds for group size (3.5 individuals), BA of hardwoods $7.6-22.9$ cm dbh (0.97 m²/ha), and BA of pines ≥ 35.6 cm dbh (5.1 m²/ha); the ranked importance for these habitat thresholds was the same as in the full tree. The threshold for BA of pines $25.4-35.6$ was not retained in the pruned tree due to a high error rate relative to the mean fledgling production (mean fledgling production = 0.5; mean square error = 0.583) for the sample size ($n = 6$; Fig. 2).

4.2. Applying QCA to regression tree results

Synthesizing results from the full regression tree using QCA revealed RCW foraging habitat threshold-fitness relationships are contingent on group size and hardwood midstory conditions. Groups with above- or below-average fledgling production typically were consistently similar with respect to the presence and absence of group size and hardwood midstory BA threshold conditions, respectively (Table 2). In other words, individual RCW groups with above-average fledgling production were consistently large (> 3 individuals) and had home ranges with BA of hardwood midstory trees < 0.97 m²/ha.
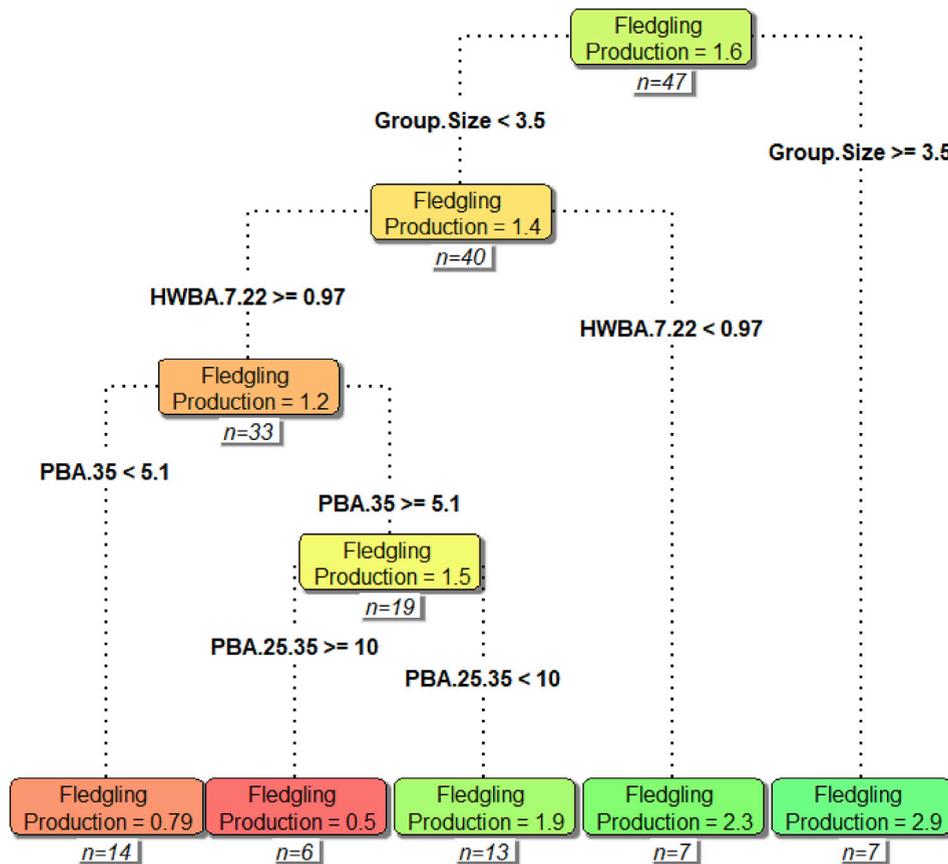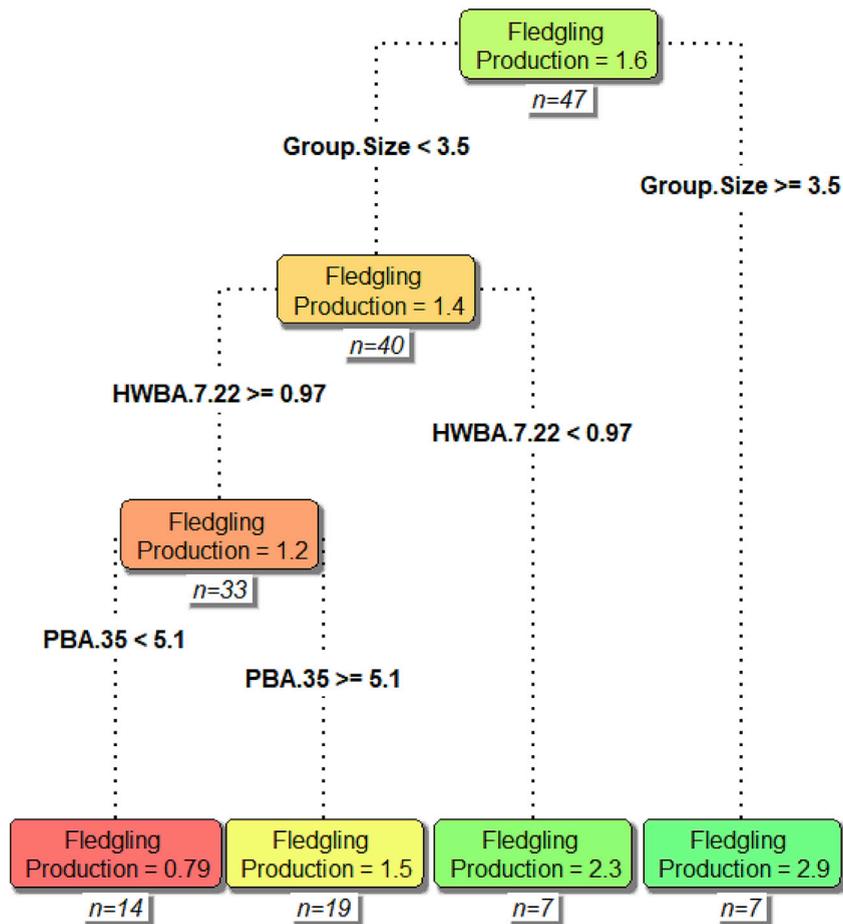
Fig. 1. The full regression tree for evaluating relationships between red-cockaded woodpecker fledgling production, group size, and average habitat conditions within woodpecker home ranges. Each node is labelled with the average fledgling production and sample size of woodpecker groups. Each branch is labelled with the habitat metric and associated threshold value that leads to either above- or below-average fledgling production. PBA = pine basal area (m^2/ha); HWBA = hardwood basal area. Numbers following basal ar variables represent dbh size classes.

Additionally, QCA revealed alternative combinations of habitat thresholds that in conjunction with group size consistently lead to above-average reproductive success and covered approximately 88% of all cases (Table 3). The QCA parsimonious solution indicates consistent above-average fledgling production ($\geq$ 1.6 fledglings/group) can occur in habitat with BA of pines $\geq$ 35.6 cm dbh $\geq$ 5.1 m^2/ha or BA of pines 25.4–35.6 cm dbh $\geq$ 10 m^2/ha (Table 3). Of particular importance is that QCA retained BA of pines 25.4–35.6 cm dbh $\geq$10 m^2/ha as a necessary and sufficient condition in the parsimonious solution, but only in conjunction with group size and in the absence of habitat satisfying thresholds for BA of pines $\geq$ 35.6 cm dbh $\geq$ 5.1 m^2/ ha (Table 3). In other words, increases in RCW fitness with provision of habitat satisfying thresholds for pines 25.4–35.6 cm dbh ($\geq$ 10 m^2/ha) is contingent on the presence of large groups ($>$ 3), the presence of a minimal hardwood midstory, and the absence of threshold conditions for pines $\geq$ 35.6 cm dbh. The importance of threshold conditions for pines 25.4–35.6 cm dbh in conjunction with group size and pines $\geq$ 35.6 cm dbh was not retained in the pruned regression tree due small sample sizes.

5. Discussion

The QCA results from this study indicate multiple combinations of foraging habitat thresholds in conjunction with group size effects can consistently lead to above-average reproductive success for RCWs on SRS, and these combinations may not be captured by correlative models. For instance, our finding that pines 25.4–35.6 cm dbh can be sufficient for above-average reproduction, even without pines $\geq$ 35.6 cm dbh, was not detected in previous correlative studies in this region (Spadgenske et al., 2005; Garabedian et al., 2017). This novel combination of thresholds discovered using QCA may explain why availability of large and old pines does not always improve predictive power of correlative habitat-fitness models (James et al., 1997). Lack of large pines in certain populations can limit reproductive success, but lack of large pines does not fully account for below-average reproductive success by itself because it operates in conjunction with hardwood midstory encroachment, medium pines, and group size. Benefits associated with large and medium pine size classes are also important in the context of geographic variation in habitat structure and fitness relationships, and impacts on range-wide habitat

Fig. 2. The pruned regression tree for evaluating relationships between red-cockaded woodpecker fledgling production, group size, and average habitat conditions within woodpecker home ranges. Each node is labelled with the average fledgling production and sample size of woodpecker groups. Each branch is labelled with the habitat metric and associated threshold value that leads to either above- or below-average fledgling production. PBA = pine basal area (m²/ha); HWBA = hardwood basal area. Numbers following basal area variables represent dbh size classes.

Table 3
Consistency and coverage scores for necessary, sufficient, and parsimonious combinations of habitat threshold conditions that lead to above-average reproductive success of individual red-cockaded woodpecker groups ($n = 47$) on the Savannah River Site, South Carolina, USA.

Solution Terms[a]	Consistency	Coverage	Unique coverage[b]
Necessary conditions			
GROUP + HWMID	0.963	0.578	
HWMID + PINES≥35	0.963	0.565	
GROUP + PINES≥35	0.926	0.694	
GROUP + pines25-35	0.926	0.625	
Sufficient conditions			
HWMID	0.900	0.333	
GROUP * PINES≥35 * pines25-35	1.00	0.148	
GROUP * pines≥35 * PINES25-35	1.00	0.074	
Parsimonious solution	**0.727**	**0.889**	
HWMID +	0.900	0.334	0.037
GROUP +	0.800	0.593	0.185
PINES≥35 * pines25-35 +	0.786	0.407	0.259
pines≥35 * PINES25-35	0.667	0.074	0.012

[a] The symbol '*' is referred to as 'AND' and the symbol '+' as 'OR'. Uppercase text indicates the threshold condition is present while lowercase text indicates the threshold condition is absent. Numbers following pine variables represent dbh size classes. Hardwood midstory (HWMID) is the basal area (BA; m²/ha) of hardwood trees 7.6–22.9 cm dbh. Group size (GROUP) is the total number of individuals in the group. Threshold conditions for group size were present if group sizes were > 3, threshold conditions for hardwood midstory were present if BA was < 0.97 m²/ha, threshold conditions for pines ≥ 35 cm dbh were present if BA was ≥ 5.1 m²/ha, and threshold conditions for pines 25–35 cm dbh were present if BA was ≥ 10 m²/ha.

[b] Unique coverage reflects the proportion of cases exhibiting the specific combination of terms included in the parsimonious solution.

correlative models such as the RCW Matrix (McKellar et al., 2014). Identifying the fitness benefits associated with provision of habitat satisfying thresholds for pines $\geq$ 35.6 cm dbh or 25.4−35.6 cm dbh is important for assessment of potential RCW habitat as well because both pine size classes can have positive effects on RCW group productivity (Garabedian et al., 2014b; McKellar et al., 2014, 2015; Walters et al., 2002). Based on our study, QCA is likely to identify unique combinations of threshold conditions that are sufficient for above-average productivity, even when habitat quality may be largely determined by the presence or absence of a single threshold (e.g., thresholds for pines $\geq$ 35.6 cm dbh for RCWs on SRS; Garabedian et al., 2014a). By identifying unique and potentially uncommon combinations of conditions that lead to the shared positive outcomes across groups, QCA facilitates development of new hypotheses to test in future research.

The overall importance of group size in the QCA more broadly illustrates the importance of accounting for complex interactions between demographics and habitat structure when evaluating habitat management effects on fitness for a small number of focal groups. Using QCA, we were able to detect positive group size interaction effects associated with thresholds for pines 25.4−35.6 cm dbh where thresholds for pines $\geq$ 35.6 cm dbh were absent, even though there was only a single group exhibiting this unique combination of conditions in the SRS dataset. The rarity ($n = 1$) of this novel combination of thresholds renders it almost impossible to discover using correlative studies. Large groups typically represent a small fraction of the population in many group-living species (Griesser et al., 2011; Jovani and Mavor, 2011), but may provide key insights on the importance of unique combinations of habitat and group size conditions that cannot be detected in correlative models due to small sample sizes. Doerr and Doerr (2007) determined that larger groups had positive effects on reproduction in brown treecreepers (*Climacteris picumnus*) even after controlling for habitat quality, but noted that small sample sizes precluded fitting higher-order interactions with breeder age that may have confounded relationships between group size and habitat quality. Controlled comparisons offer an approach to account for group size effects by holding territory quality or breeding individuals constant. However, controlled comparisons typically can only utilize a small portion of data on group-living species, and thus often lack adequate statistical power to identify key combinations of group size and habitat conditions (Carrete et al., 2008). Limited statistical power in controlled comparisons among focal individuals in some studies indicated that excessively stringent habitat requirements, and ultimately greater effort dedicated to increasing territory quality, was needed to maintain high annual productivity (Ferrer and Bisson, 2003; Penteriani et al., 2004). In contrast, QCA analysis in our study indicated that group size tends to have larger effects on RCW fitness than habitat structure, and thus indicates greater management focus should be placed on promoting large group sizes. This could be accomplished for RCWs by enhancing demographic connectivity through strategic placement of recruitment clusters within 400 m of existing clusters occupied by RCW groups (Garabedian et al., 2018b). Based on results from this study, QCA may be well-suited for synthesis of habitat-fitness data for group-living species like RCWs and brown treecreepers because group size and breeder age can have a large positive effect on fitness independent of habitat conditions (Meade et al., 2010).

Because QCA is not constrained by collinearity, we could identify how large and medium pines can have consistent positive effects on RCW group fitness in conjunction with group size and hardwood midstory conditions, without fitting compound habitat variables or introducing bias from collinearity. This would not have been possible with traditional correlative methods because BA of large and medium pines were collinear. Collinear habitat variables have been recognized as potential confounding factors in multiple regression models applied in previous RCW habitat-fitness research (James et al., 1997, 2001). Compound habitat variables can represent interaction effects for collinear variables (e.g., large and medium pines in RCW foraging habitat), but interpretation of effects of compound variables is challenging and difficult to translate into management recommendations (James et al., 2001). The ability to understand such complex interactions using QCA can help test additional hypotheses about habitat-fitness relationships in other systems. For instance, density-dependent reproduction in the cooperatively breeding Seychelles warbler (*Acrocephalus sechellensis*) may be driven by territory quality, group size, or breeder quality (e.g., age), which have been shown to correlate for many species, thus complicating use of correlative models (Brouwer et al., 2009).

In some cases, species-specific QCA results may vary depending on the benchmark variable selected to define a successful conservation outcome. We used above-average fledgling production as the successful outcome in the QCA to support RCW foraging habitat management because fledgling production directly relates to habitat structure and group size (McKellar et al., 2014; USFWS, 2003; Walters et al., 2002). Alternative fitness metrics can be used to define a successful conservation outcome, which may be important because a single habitat management strategy could have contrasting effects on different metrics (Pidgeon et al., 2006). For example, maintaining semi-open bush land for pale-headed brushfinch (*Atlapetes pallidiceps*) using prescribed fire was shown to improve reproduction by reducing woody encroachment and increasing forage availability, but at the expense of survival because territories lacked sufficient cover and forage during the non-breeding season (Hartmann et al., 2015). Hence, to support habitat management strategies for other species, it may be more useful to define successful conservation outcomes using benchmarks for vital rates other than reproduction (Colchero et al., 2009; Hilbers et al., 2017; Mumme et al., 2015). Alternatively, to provide conservation support in the context of species' reintroductions, successful conservation outcomes may be defined using benchmarks for retention of translocated birds (Franzreb, 2004, 1999), dispersal success (Trainor et al., 2013), or inbreeding rates (Schiegg et al., 2006). QCA may be particularly useful for research on conditions that consistently lead to successful species reintroductions where small sample sizes are common (Bennett et al., 2012; Canessa et al., 2016). For RCW reintroductions, small sample sizes (i.e. < 30 individuals translocated) and complex interactions among demographic, social, and habitat conditions that can influence reintroduction success (Carrie et al., 1999; Cox and McCormick, 2016; Kesler and Walters, 2012) rendering QCA a potentially valuable research tool.

QCA provides a relatively straightforward approach to support conservation decisions for endangered species that can be employed with limited data. A main advantage of QCA is the ability to simplify complex interactions among habitat features and demographics that have been intractable due to stringent data requirements of parametric correlative models. QCA has been demonstrated effective in simplifying complex interactions among factors that determine effectiveness of marine protected areas at protecting species richness (Rudd, 2015) and factors contributing to deforestation (Porter-Bolland et al., 2012; Rudel, 2008). Our case study on RCW foraging habitat-fitness relationships demonstrates QCA similarly can improve decision support for species-specific conservation. Our study suggests QCA can offer an intuitive framework for modeling collinear habitat attributes, and alleviate the need for complex interaction effects in correlative models. The emphasis placed on qualitative combinations of conditions prevents focus on the statistical significance of individual species-habitat results that has precluded development of formal meta-analytic models of RCW foraging habitat-fitness relationships (Garabedian et al., 2014b). The unique combinations of habitat threshold conditions in conjunction with RCW group size suggests practitioners should view the full set of RCW foraging habitat guidelines as a general template for habitat quality that can be catered to site-specific relationships with fitness. QCA can be extended to address many complex issues in endangered species recovery, ranging from effects of energy development on critical habitat (Doherty et al., 2018) to factors influencing success of species reintroductions (Bennett et al., 2013).

In conclusion, our case study on RCW foraging habitat-fitness relationships demonstrates QCA can identify unique combinations of habitat and group size conditions that consistently lead to reproductive success even when small sample sizes preclude formal correlative analyses and other quantitative approaches to data synthesis. To achieve consistent above-average fledgling production among individual RCW groups, we recommend RCW managers target larger groups sizes (> 3 individuals) and hardwood midstory BA < 0.97 m^2/ha within home ranges. Where group sizes are > 3, and hardwood midstory BA is < 0.97 m^2/ha within home ranges, managers can target provision of habitat with ≥ 5.1 m^2/ha BA of pines ≥ 35.6 cm dbh or, alternatively, with ≥ 10 m^2/ha BA of pines $25.4-35.6$ cm dbh to achieve consistent above-average fledgling production among individual groups.

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