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Life history trait differences in isolated populations of the endangered Red-cockaded Woodpecker

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Abstract Changes in life history traits can reveal adaptations to changing environments. Red-cockaded Woodpeckers *(Picoides borealis)* are cooperative breeders that have specific reproductive habitat needs. We examined three separate sites in the southeastern United States to see how life history traits differed among isolated populations of Red-cockaded Woodpeckers from 1980 to 2013. We examined the life history traits group size, partial brood loss, number of fledglings, lay date, clutch size, and lifespan. Traits differed among sites, suggesting that populations were adapted to local conditions and different life history trade-offs were important under different environmental conditions at each site. At the two coastal sites in Florida and North Carolina, the family group sizes, lifespans, and partial brood loss were higher when compared to the inland site in North Carolina. Clutch size and number fledged were higher at the two northernmost sites when compared to the southern site. Identifying the differences in life history traits can allow more specific and effective management practices.

Keywords: clutch size, cooperative breeder, endangered, lay date, life history, Red-cockaded Woodpecker

Összefoglalás Az életmenet jellemzők változásai a környezethez való adaptációt mutathatnak. A kooperatívan költő kokárdás harkály *(Picoides borealis)* élőhely-specialista faj. Az Amerikai Egyesült Államok délkeleti részén, három területen vizsgáltuk, hogy az életmenet bizonyos elemei különböznek-e a vizsgált faj izolált populációi között. Az adatokat 1980–2013-ig gyűjtöttük. Az életmenet következő szegmenseit vizsgáltuk: csoportméret, részleges fészekalj-veszteség, a kirepülő fiatalok száma, a tojásrakás dátuma, fészekalj méret és az élettartam. A felsorolt változók területenként eltéréseket mutattak, sugallva, hogy az egyes populációk adaptálódtak a helyi viszonyokhoz, illetve, hogy az egyes életmenet szegmensek különböző súllyal eshetnek latba az egyes területeken. A két tengerparti területen, Floridában és Észak-Karolinában a csoport mérete, az egyedek élethossza és a részleges fészekalj vesztesége magasabb volt a kontinentális észak-karolinai területhez képest. A fészekalj mérete és a kirepült fiatalok száma ezzel szemben magasabb volt a két északi populáció esetében. Az életmenet jellemzők populációk közötti különbségeinek felderítése lehetővé teszi specifikusabb, effektívebb természetvédelmi kezelések alkalmazását.

Kulcsszavak: fészekaljméret, kooperatív költő, veszélyeztetett, tojásrakási dátum, életmenet, kokárdás harkály

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Introduction

Life history strategies directly affect individual fitness. Examples of key life history traits include clutch size, lifespan, and age at first reproduction (Stearns 1976). Variation in life history traits, such as clutch size, can be determined by factors such as resource availability and environment (Lack 1947). Associations, often negative, between life history traits are referred to as life history trade-offs (Zera & Harshman 2001). Different life history trade-offs and trait values are selected for in different environments (Linden & Møller 1989) even within a single species. For example, life history strategies can vary over elevational gradients within species (Bears *et al.* 2009). The combination of life history trade-offs should result in the highest fitness for individuals under those conditions (Badyaev & Ghalambor 2001), and these individuals will be better represented than their conspecifics in future generations (Stearns 1976). Therefore, examining life history traits is important both because life history theory is a major branch in ecology and because it can assist in conservation and management efforts.

This study investigated life history trait differences among three populations of endangered Red-cockaded Woodpeckers *(Picoides borealis)* for which extensive long-term data were available. In the past decade, the majority of studies on Red-cockaded Woodpeckers focused on habitat requirements and preferences over just a few years. Demographic information obtained from studies conducted over longer periods of time can be beneficial for identifying life history traits that should be targeted for management. Since 1980 (Walters *et al.* 1988), we have monitored three fragmented populations of Red-cockaded Woodpeckers that occur in different locations. These three populations have been managed separately and comparisons among them could reveal differences that can be used to improve site-specific management techniques. Red-cockaded Woodpeckers occur in isolated populations and face different quality habitats, climates, and management regimes. Better management can be achieved by focusing on the different life history strategies and trade-offs utilized at these fragmented sites. Therefore, assessment of life history traits is essential to understanding how different management techniques are affecting populations.

Methods

Study species

Red-cockaded Woodpeckers are cooperative breeders, with 0–4 helpers assisting a single, monogamous breeding pair in defending territories, raising young, and excavating new cavities (Lennartz *et al.* 1987). Most helpers are male offspring from previous breeding seasons, but female offspring and unrelated helpers of both sexes also occur (Walters *et al.* 1988). Red-cockaded Woodpeckers are non-migratory and family groups defend their territories year round. They are a medium-sized woodpecker that eats mostly invertebrates, and clutch sizes vary from 2–5 eggs.

Red-cockaded Woodpeckers inhabit mature, open pine stands throughout the southeastern United States (Schaefer *et al.* 2004). Due to the reduced use of fire and the cutting of

old-growth pine forests in the Southeast, the range and numbers of Red-cockaded Woodpecker have declined (Schaefer *et al.* 2004). Management of Red-cockaded Woodpeckers has focused on improvement of habitat quality to encourage continued use of territories and addition of new territories. Territories are defended areas that contain a woodpecker family group's activities and its borders may be determined by habitat edges or by other woodpecker groups (Ligon 1970). Each territory contains a set of actively used and defended cavity trees termed the cavity tree cluster (Walters *et al.* 1988, Walters *et al.* 1992). Red-cockaded Woodpeckers are unique in excavating their cavities exclusively in living pine trees. The presence of high quality cavities has been shown to be a critical component of territory quality (Walters *et al.* 1992), presumably due to the difficulty and inordinate length of time required to excavate cavities in living pines (James *et al.* 1997, Harding & Walters 2004). Accordingly, artificial cavities have been used to maintain (i.e. prevent territory abandonment) and improve (i.e. convert unsuitable habitat to suitable habitat) territories (Walters 1991) with great success.

Study Areas

In this study, we used long-term demographic data from three isolated study sites: an inland site in the longleaf pine *(Pinus palustris)* forests of the North Carolina Sandhills (SH), a coastal site of longleaf and loblolly pine *(Pinus tueda)* at Marine Corps Base Camp Lejeune, NC (MCBCL), and a Gulf Coast Florida panhandle site at Eglin Air Force Base, Florida (EAFB) with extensive longleaf pine sandhills habitat *(Map 1)*. Detailed descriptions of the study areas and habitat can be found as follows: North Carolina Sandhills (Carter *et al.* 1983, Walters *et al.* 1988); North Carolina Coastal Plain (Walters *et al.* 1995, Zwicker & Walters 1999) and Eglin Air Force Base (Blanc & Walters 2008).

The inland site (Sandhills, NC) was once dominated by fire-dependent species such as longleaf pines. The other forests are mixed pine and have varying amounts of understory and midstory (Trainor *et al.* 2013). Data were collected during the breeding seasons (April-June) from 1980 to 2013.

Field methods

The demographic data were obtained by monitoring color-marked birds at each site for up to 32 years: coastal Marine Corps Base Camp Lejeune (1986–2011), inland Sandhills (1980–2011), and coastal Eglin Air Force Base (1993–2013). For a detailed description of how data were collected, refer to Walters *et al.* (1988).

Briefly, each year, members of each territory and unaffiliated birds were individually identified by color band combinations and their status (i.e. breeder, helper, floater) was determined (Letcher *et al.* 1998). All active cavities within a cluster were marked and checked repeatedly during the breeding season for signs of nesting, to age nestlings for banding, and to identify fledglings (Walters *et al.* 1988). Reproduction was monitored by identifying and counting banded and fledged young in each territory.
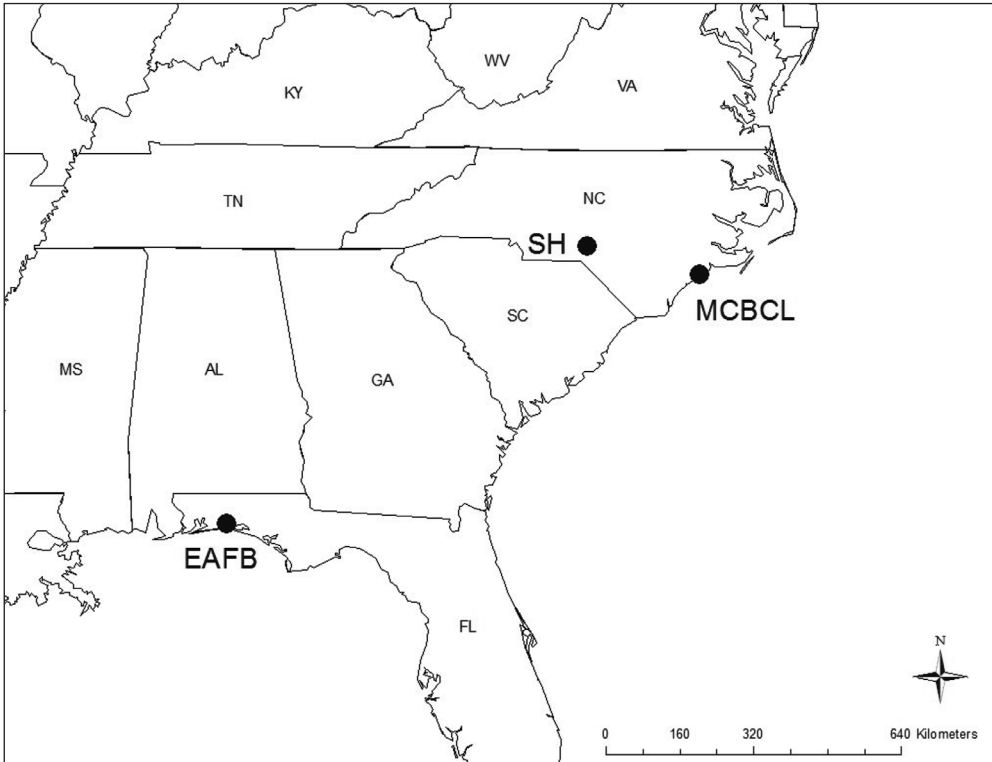
Map 1.   Map of the southeastern United States showing the three Red-cockaded Woodpecker study sites: Sandhills (SH), Marine Corps Base Camp Lejeune (MCBCL), Eglin Air Force Base (EAFB)

1. térkép Az Amerikai Egyesült Államok délkeleti részének térképe a vizsgált területekkel: homokdombok (SH), Lejeune haditengerészeti bázis (MCBCL), Eglin légierő bázis (EAFB)

Statistical analyses

We used Generalized Linear Mixed Models (GLMM), Generalized Linear Models (GLM), and Linear Mixed Models (package lme4) (Bates *et al.* 2015) in program R (R Core Team 2014) to compare traits among sites. The life history traits that we examined were group size, lifespan, number of fledglings, clutch size, lay date, and brood loss (eggs laid – eggs hatched). To examine lifespan, we only included birds that survived the first year and hatched before 2001, as only 0.7% (13/1891) of birds hatched before 2001 were still alive in 2013. For lay date, only the first nesting attempt was used. Red-cockaded Woodpeckers typically only re-nest after nest failure. The Eglin Air Force Base data set lacked information on lay date due to differences in monitoring protocols, and was therefore not included in the analysis. Group size included the breeding pair and adult helpers. Except for lifespan, each response variable was treated as a feature of the group, not of the breeders. Therefore, only one observation per territory was included in the analyses. For each dependent variable, we included the variable Site (Sandhills, Marine Corps Base Camp Lejeune, or Eglin Air Forde Base) to examine differences between study sites. We also included other possible predictor variables (covariates) that could explain

variation in life history traits in each model as appropriate. The covariates were group size (but not when group size was the response variable), sex, age, and mate's age. We also included the following random effects: individual identity of the male territory holder, territory and microsite. Microsites were groups of territories that were geographically near each other within each study area. We included different random factors in each analysis depending on how the data were structured and which random factors explained >0 variance. To limit the number of possible models and to avoid problems with model convergence, we did not examine interactions in this analysis (Hoyt & Hannon 2002, Montague-Drake *et al.* 2009). We used a Poisson distribution with a log link for group size, lifespan, number of fledglings, clutch size, and brood loss. We used a Gaussian distribution with an identity link for lay date. We used Akaike's Information Criterion for small sample sizes (AICc) to compare models and to determine if life history traits differed among sites (Burnham & Anderson 2002, Anderson 2008). We used maximum likelihood estimation for the AIC analyses, but estimates were based on restricted maximum likelihood estimation. We tested saturated GLMMs and GLMs for overdispersion by examining the ratio of the deviance to residual degrees of freedom, but the ratios were <1, indicating the data were not overdispersed. All reported estimates and graphs are predicted values for each site from the highest-ranked model and 95% confidence intervals.

Results

Overall, there were 41,396 total observations and 4,514 individual birds. Marine Corps Base Camp Lejeune (coastal site) had the lowest number of birds with 6,754 total observations for 565 individual birds. At Eglin Air Force Base (coastal site), there were 835 individual birds and 2,508 observations. The Sandhills site (inland site) was studied for the most years and had 3,114 individual birds and 32,134 total observations.

Group sizes were larger in the two coastal sites (MCBCL 2.88 adults, 95% CI: 2.79-2.97; EAFB 2.81 adults, 95% CI: 2.66-2.98) than at the inland site (SH 2.64 adults, 95% CI: 2.61-2.68) *(Table 1, Figure 1)*. However, variance at the Eglin site was quite high, with large confidence intervals. Lifespan was longest at Marine Corps Base Camp Lejeune (6.02 years, 95% CI: 5.72-6.33) and was shorter in the inland Sandhills population (4.63 years, 95% CI: 4.52-4.74) *(Table 2, Figure 2)*. The Florida population (Eglin Air Force Base) fell in between with a lifespan of 5.21 (95% CI: 4.30-6.32) years.

Clutch size was significantly larger in the two northern populations (MCBCL 3.41 eggs, 95% CI: 3.29-3.53; SH 3.31, 95% CI: 3.26-3.37) than in the more southern Florida population (EAFB; 2.99, 95% CI: 2.76-3.23) *(Table 3, Figure 3)*. Fledgling production was also significantly higher in the northern populations (SH 1.79 fledglings per breeding male, 95% CI: 1.75-1.83; MCBCL 1.66, 95% CI: 1.58-1.75), compared to the Florida population at Eglin Air Force Base (1.25, 95% CI: 1.10-1.41) *(Table 4, Figure 4)*. Lay dates were earlier in the inland Sandhills population (Julian date 118, 95% CI: 117-120) than the coastal Marine Corps Base Camp Lejeune population (125, 95% CI: 122-128) *(Table 5, Figure 5)*. The coastal sites experienced more brood loss (MCBCL 1.38 eggs lost, 95% CI: 1.31-1.45; EAFB 1.38 eggs lost, 95% CI: 1.26-1.51) than the inland Sandhills population (1.12 eggs lost, 95% CI: 1.09-1.14) *(Table 6, Figure 6)*.

Model (Group Size)	K	AICc	Delta_AICc	LL	Cum.Wt
Site + Territory	4	2390.116	0	-1191.06	0.999999
Territory	2	2418.464	28.347	-1207.23	1

Table 1. Comparison of models examining whether group size differs between study sites in Red-cockaded Woodpeckers (n=9,620). Territory was treated as a random factor. LL is the log likelihood, Cum. Wt is the cumulative Akaike weight of each model

1. táblázat Az egyes vizsgálati területeken rögzített csoportméreteket vizsgáló modellek összehasonlítása a kokárdás harkálynál (n=9620). A territórium random faktorként volt kezelve. Az LL log likelihood-ot jelent, a Cum. Wt pedig az egyes modellek Akaike (AIC, Akaike információs kritérium) súlyát jelenti
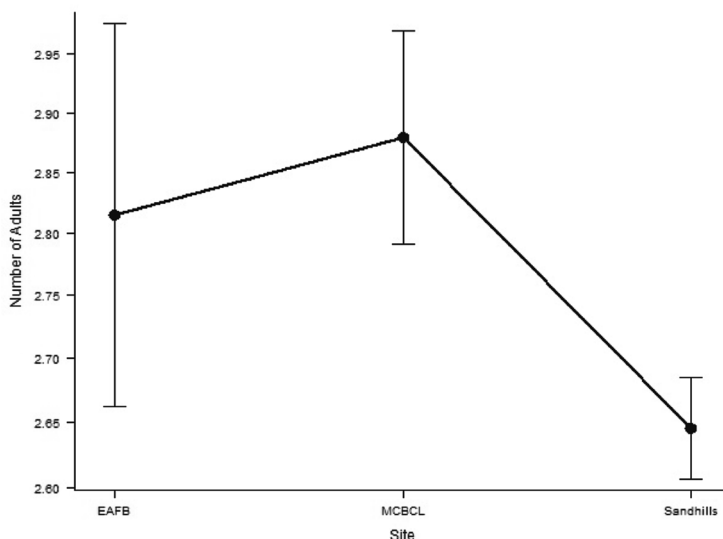

Figure 1. Group sizes (number of adults) were larger at the two coastal sites (Marine Corps Base Camp Lejeune and Eglin Air Force Base) when compared to the inland site (Sandhills). Estimates are predicted values from the highest ranked model with 95% confidence intervals

1. ábra A csoportméret (adult egyedek száma) a két tengerparti területen nagyobb volt (Lejeune haditengerészeti bázis és Eglin légierő bázis), összehasonlítva a kontinentális vizsgálati területtel (homokdombok). A becslések a lejobbnak értékelt modellből prediktált értékek, 95%-os konfidencia intervallumokkal. A vízszintes tengelyen olvashatók az egyes mintaterületek: Eglin légierő bázis (EAFB), Lejeune haditengerészeti bázis (MCBCL), homokdombok (SH)

Model (Lifespan)	K	AICc	Delta_AICc	LL	Cum.Wt
Site + Mean Group Size + Sex	**5**	**8579.668**	**0**	**-4284.82**	**1**
Mean Group Size + Sex	3	8658.296	78.628	-4326.14	1
Site + Mean Group Size	4	9136.866	557.198	-4564.42	1
Mean Group Size	2	9228.221	648.552	-4612.11	1
Site + Sex	4	9286.221	706.553	-4639.10	1
Site	3	9856.622	1276.954	-4925.30	1
Sex	2	9881.042	1301.374	-4938.52	1
1	1	10447.000	1867.333	-5222.50	1

Table 2.   Comparison of models examining factors that affect Red-cockaded Woodpecker lifespan (n=2,583). All factors were fixed. LL is the log likelihood, Cum. Wt is the cumulative Akaike weight of each model

2. táblázat A kokárdás harkály élettartamát (n=2583) befolyásoló faktorokat vizsgáló modellek öszszehasonlítása. Minden faktor fix volt. Az LL log likelihood-ot jelent, a Cum. Wt pedig az egyes modellek Akaike (AIC, Akaike információs kritérium) súlyát jelenti
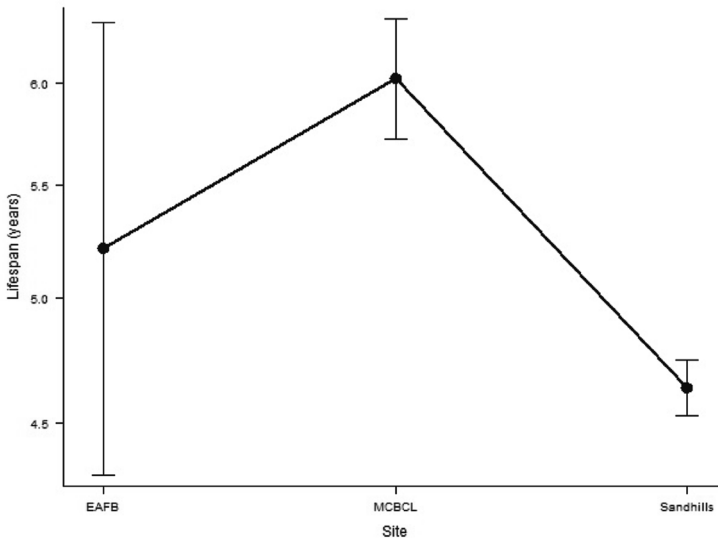

Figure 2. Lifespan was longest at Marine Corps Base Camp Lejeune, and shortest at the inland study site (Sandhills). Estimates are predicted values from the highest ranked model with 95% confidence intervals

2. ábra   Az egyedek élettartama a Lejeune haditengerészeti bázis területén volt a leghosszabb, a legrövidebb pedig a kontinentális területen (homokdombok). A becslések a lejobbnak értékelt modellből prediktált értékek, 95%-os konfidencia intervallumokkal. A vízszintes tengelyen olvashatók az egyes mintaterületek: Eglin légierő bázis (EAFB), Lejeune haditengerészeti bázis (MCBCL), homokdombok (SH)

Model (Clutch size)	K	AICc	Delta_AICc	LL	Cum.Wt
Site + Group Size + Age + Bird ID	**6**	**1018.886**	**0**	**-503.44**	**0.916027**
Group Size + Age + Bird ID	4	1023.925	5.039	-507.96	0.989784
Site + Age + Bird ID	5	1027.999	9.113	-508.99	0.999401
Age + Bird ID	3	1033.551	14.665	-513.77	1
Site + Group Size + Bird ID	5	1053.968	35.081	-521.98	1
Group Size + Bird ID	3	1059.220	40.334	-526.61	1
Site + Bird ID	4	1070.644	51.758	-531.32	1
Bird ID	2	1076.509	57.623	-536.25	1

Table 3.   Comparison of models examining factors that affect Red-cockaded Woodpecker clutch size (n=5,428). Individual bird identity (Bird ID) was included as a random factor. LL is the log likelihood, Cum. Wt is the cumulative Akaike weight of each model

3. táblázat A kokárdás harkály fészekaljméretét (n=5428) befolyásoló faktorokat vizsgáló modellek összehasonlítása. A madarak egyéni azonosítója (Bird ID) random faktorként volt kezelve. Az LL log likelihood-ot jelent, a Cum. Wt pedig az egyes modellek Akaike (AIC, Akaike információs kritérium) súlyát jelenti
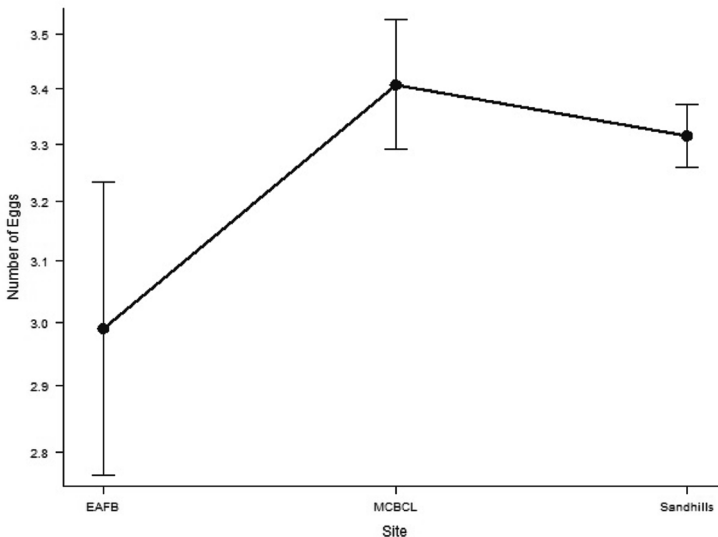

Figure 3.   The number of eggs (clutch size) was larger at the two northernmost sites (coastal Marine Corps Base Camp Lejeune and the inland Sandhills site) compared to Eglin Air Force Base in coastal Florida. Estimates are predicted values from the highest ranked model with 95% confidence intervals

3. ábra   A tojások száma (fészekaljméret) a két északi mintaterületen (Lejeune haditengerészeti bázis és homokdombok) nagyobb volt az Eglin légierő bázisnál tapasztaltakhoz képest. A becslések a lejobbnak értékelt modellből prediktált értékek, 95%-os konfidencia intervallumokkal. A vízszintes tengelyen olvashatók az egyes mintaterületek: Eglin légierő bázis (EAFB), Lejeune haditengerészeti bázis (MCBCL), homokdombok (SH)

Model (Fledglings)	K	AICc	Delta_AICc	LL	Cum.Wt
Site + Group Size + Age + Bird ID	**6**	**4885.538**	**0**	**-2436.76**	**1**
Group Size + Age + Bird ID	4	4924.064	38.525	-2458.03	1
Site + Group Size + Bird ID	5	5048.455	162.917	-2519.22	1
Site + Age + Bird ID	5	5061.142	175.604	-2525.57	1
Age + Bird ID	3	5089.991	204.453	-2541.99	1
Group Size + Bird ID	3	5090.812	205.273	-2542.40	1
Site + Bird ID	4	5280.114	394.576	-2636.05	1
Bird ID	2	5307.040	421.501	-2651.52	1

Table 4. Comparison of models examining factors that affect the number of fledglings produced in Red-cockaded Woodpeckers (n=5,428). Individual bird identity (Bird ID) was included as a random factor. LL is the log likelihood, Cum. Wt is the cumulative Akaike weight of each model

4. táblázat A kokárdás harkály kirepülési számát (n=5428) befolyásoló faktorokat vizsgáló modellek összehasonlítása. A madarak egyedi azonosítója (Bird ID) random faktorként volt kezelve. Az LL log likelihood-ot jelent, a Cum. Wt pedig az egyes modellek Akaike (AIC, Akaike információs kritérium) súlyát jelenti
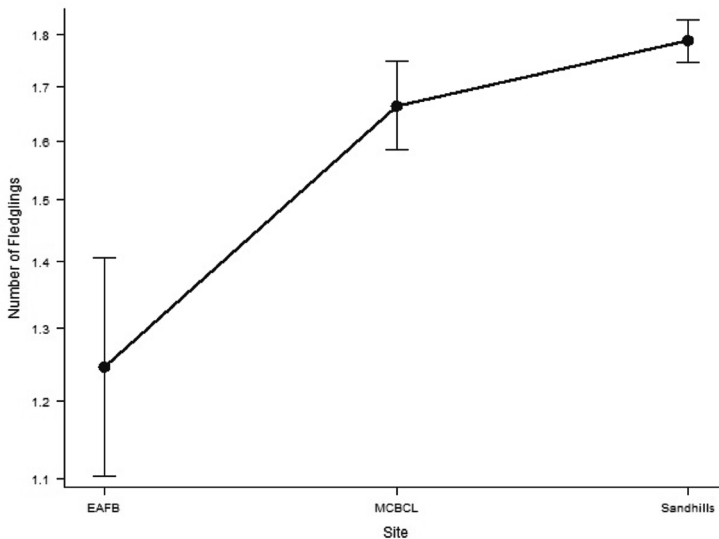

Figure 4. The mean number of fledglings was larger at the two northernmost sites (coastal Marine Corps Base Camp Lejeune and the inland Sandhills study site) compared to the coastal site in Florida (Eglin Air Force Base). Estimates are predicted values from the highest ranked model with 95% confidence intervals

4. ábra A kirepült egyedek átlagos száma magasabb volt a két északi mintaterületen (Lejeune haditengerészeti bázis és homokdombok). A becslések a legjobbnak értékelt modellből prediktált értékek, 95%-os konfidencia intervallumokkal. A vízszintes tengelyen olvashatók az egyes mintaterületek: Eglin légierő bázis (EAFB), Lejeune haditengerészeti bázis (MCBCL), homokdombok (SH)

Model (Lay Date)	K	AICc	Delta_AICc	LL	Cum.Wt
Site + Age + Mate's Age + Microsite	**5**	**2440.191**	**0**	**-1215.09**	**0.891347**
Age + Mate's Age + Microsite	4	2444.400	4.209	-1218.19	1
Site + Mate's Age + Microsite	4	2809.978	369.787	-1400.98	1
Mate's Age + Microsite	3	2813.886	373.695	-1403.94	1
Site + Age + Microsite	4	3407.092	966.901	-1699.54	1
Age + Microsite	3	3410.560	970.369	-1702.28	1
Microsite	2	4045.547	1605.356	-2020.77	1
Site + Microsite	3	4042.444	1602.253	-2018.22	1

Table 5.   Comparison of models examining factors that affect Red-cockaded Woodpecker lay date (n=5,215). Microsite (geographic location within each study site) was included as a random factor. LL is the log likelihood, Cum. Wt is the cumulative Akaike weight of each model

5. táblázat A kokárdás harkály tojásrakási dátumát (n=5215) befolyásoló faktorokat vizsgáló modellek összehasonlítása. A vizsgálati területen belüli pozíció (Microsite) random faktorként volt kezelve. Az LL log likelihood-ot jelent, a Cum. Wt pedig az egyes modellek Akaike (AIC, Akaike információs kritérium) súlyát jelenti
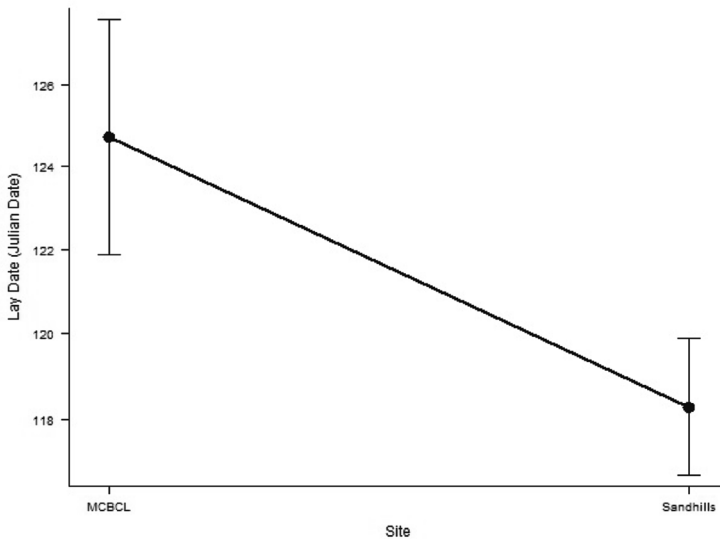

Figure 5.   Lay dates were larger (later) at coastal Marine Corps Base Camp Lejeune when compared to the inland study site (Sandhills). Estimates are predicted values from the highest ranked model with 95% confidence intervals

5. ábra   A tojásrakás későbbre esett a Lejeune haditengerészeti bázison a homokdombokhoz képest. A becslések a lejobbnak értékelt modellből prediktált értékek, 95%-os konfidencia intervallumokkal. A vízszintes tengelyen olvashatók az egyes mintaterületek: Lejeune haditengerészeti bázis (MCBCL), homokdombok (SH)

Model (Brood loss)	K	AICc	Delta_AICc	LL	Cum.Wt
Site + Territory	**4**	**5635.964**	**0**	**-2813.98**	**1**
Territory	2	5692.196	56.232	-2844.10	1

Table 6.   Comparison of models examining factors that affect Red-cockaded Woodpecker brood loss (n=7,793). Territory was treated as a random factor. LL is the log likelihood, Cum. Wt is the cumulative Akaike weight of each model

6. táblázat A kokárdás harkály fészekalj-veszteségét (n=7793) befolyásoló faktorokat vizsgáló modellek összehasonlítása. A territórium (territory) random faktorként volt kezelve. Az LL log likelihood-ot jelent, a Cum. Wt pedig az egyes modellek Akaike (AIC, Akaike információs kritérium) súlyát jelenti
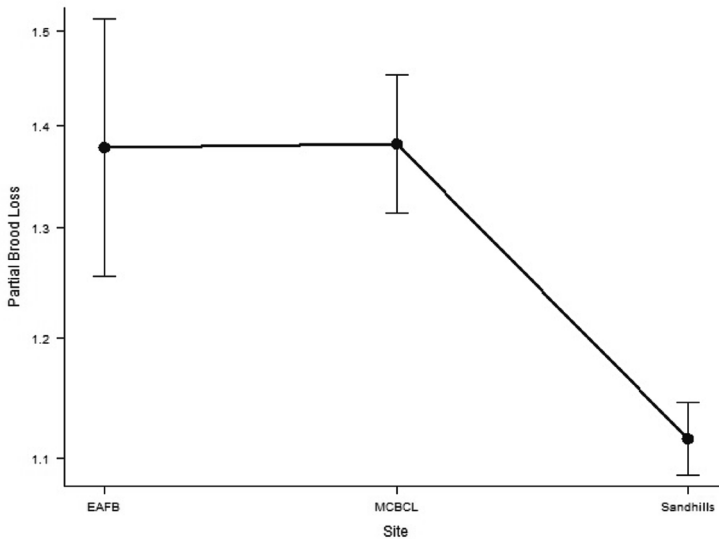

Figure 6.   The amount of brood loss was lower at the inland study site (Sandhills) when compared to the two coastal sites (Marine Corps Base Camp Lejeune and Eglin Air Force Base). Estimates are predicted values from the highest ranked model with 95% confidence intervals

6. ábra   A fészekalj-veszteség a homokdombok elnevezésű vizsgálati területen alacsonyabb volt a másik két mintaterülethez képest. A becslések a lejobbnak értékelt modellből prediktált értékek, 95%-os konfidencia intervallumokkal. A vízszintes tengelyen olvashatók az egyes mintaterületek: Eglin légierő bázis (EAFB), Lejeune haditengerészeti bázis (MCBCL), homokdombok (SH)

Discussion

Among the three Red-cockaded Woodpecker populations studied, there was ample evidence of life history variation suggesting adaptation to different conditions. The coastal populations had larger group sizes and longer lifespans compared to the inland Sandhills site, suggesting that survival is better in coastal areas than at inland sites. Group size for Red-cockaded Woodpeckers has been found to be positively correlated with fledging success (Conner *et al.* 2004), but the coastal populations experienced high brood loss despite having the largest group sizes. This could indicate that reproduction is more limited by highly variable environmental factors in coastal areas. An increase in parental care is thought to occur in order to prevent reduced survival of offspring due to adverse environmental conditions (Clutton-Brock 1991). This limitation on the number of young that survive could be a direct factor of inclement weather or due to the parents and helpers not being able to exert enough effort to properly feed and care for fledglings so that they all thrive. For example, this could be a matter of reproductive investment, with effort being limited such that fewer young survive when conditions are poorer (i.e. the same effort results in less food brought to the nest under poor conditions). Coastal storms can form from hurricanes, wave developments, depressions, and severe local storms, with the most severe damage coming from hurricanes. The southern states may experience fewer storms than the northern states, but the intensity of storms in the southern states is greater (Mather *et al.* 1964). Engstrom and Evans (1990) reported a 25% mortality in cavity trees during a hurricane year and this mortality rate was expected to be at least an order of magnitude greater than in a year in which a hurricane did not occur. Reduction of available cavities and increase in competition for cavities could force Red-cockaded Woodpeckers to roost outside of cavities and increase exposure to weather and predators, therefore weakening them or increasing chances of mortality (Engstrom & Evans 1990). The late lay date and high brood loss even with a large number of helpers could indicate that environmental factors, such as the highly variable coastal weather at Marine Corps Base Camp Lejeune, limited the number of nestlings that survived to fledging.

The southern, coastal Florida population at Eglin Air Force Base differed from the two northern populations in exhibiting lower clutch sizes and number of young fledged. The two northern populations were similar in these respects, suggesting a north-south gradient, in addition to the coastal-inland gradient discussed above, one that specifically impacts productivity. This suggests a geographic gradient in availability of resources as low food availability favors a smaller clutch and brood sizes (Ricklefs 1980, Badyaev & Ghalambor 2001). Lower food availability may be due to decreased seasonality from north to south (Ricklefs 1980). Eglin Air Force Base contains more old growth forest compared to the other sites (Varner & Kush 2004), suggesting that poor habitat is not responsible for this pattern. However, Eglin Air Force Base is known to be a low productivity site in terms of forestry metrics, so this likely is a factor (Provencher *et al.* 2001). Nevertheless, we cannot draw firm conclusions about how latitudinal gradients affect Red-cockaded Woodpecker traits given the limited number of sites in our study.

Lay dates were earlier in the Sandhills site compared to Marine Corps Base Camp Lejeune, which suggests differences in spring arrival between inland and coastal areas, as has been found elsewhere (Nilsson & Källander 2006). Group sizes were the smallest and

lifespans were shortest at the inland site (Sandhills), which may indicate that there is increased predation on adults or otherwise harsher conditions away from the coast.

These three sites in the southeastern United States have shown how different the needs of isolated populations can be within a species. To effectively manage populations, each site would benefit from conducting a study about the specific life history trade-offs a population employs. Knowing and monitoring life history traits for these managed populations can allow management efforts to be assessed by how they affect traits, or managers can focus on improving certain traits. For example, number of adults per group is associated with territory quality (Heppell *et al.* 1994, Conner *et al.* 2001, McKellar *et al.* 2014) and may be used as a secondary measure of quality, along with habitat data. Additionally, adding new territories and cavities can temporarily decrease group sizes as helpers move to the new territories (Walters 1991), so keeping track of group sizes can help managers assess the need for new territories. Many studies monitor reproductive traits such as clutch size or number fledged, and these traits can help explain population dynamics and be indicators of overall population health.

Acknowledgements

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