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RESEARCH ARTICLE

Increasing density from population recovery does not explain elevated partial brood loss in a threatened cooperative breeder

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ABSTRACT

Partial brood loss in *Dryobates borealis* (Red-cockaded Woodpecker), a federally threatened cooperative breeder in the USA, was not associated with increases in population density. Across three populations—Sandhills, North Carolina; Marine Corps Base Camp Lejeune, North Carolina; and Eglin Air Force Base, Florida—we documented no support for density-dependent effects on either early or late partial brood loss. Using long-term nest monitoring data, we evaluated multiple metrics of group size and group density in relation to brood loss at early (egg-to-nestling up to 6–10 days when banded) and late (banding-to-fledgling up to 38–40 days) stages. Reproductive outcomes did not vary with density within populations, indicating that the recent rise in partial brood loss, particularly late in the nestling period, was not driven by increasing density. While both density and partial brood loss have increased over time, these trends appear to be decoupled, highlighting the need to investigate other potential drivers of partial brood loss. Cooperative breeding can buffer reproductive output from density-related pressures through shared parental care, but as densities increase due to conservation-driven population recovery, cooperative breeders may face new or shifting constraints. Variation in reproductive outcomes may be more closely tied to site-specific factors or density-independent pressures such as weather, predation, or habitat quality. As *D. borealis* populations continue to grow under ongoing recovery efforts, understanding the mechanisms behind partial brood loss remains critical for refining conservation strategies. Our results add to growing evidence that density-dependent effects on reproduction are not universal; increasing density, though a conservation success, does not necessarily lead to reduced productivity or increased brood loss.

Keywords: cooperative breeding, density dependence, *Dryobates borealis*, partial brood loss, reproductive success

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LAY SUMMARY

- We studied whether increasing population density affects partial brood loss (when some, but not all, eggs or chicks fail to survive) in the federally threatened, cooperatively breeding *Dryobates borealis* (Red-cockaded Woodpecker).
- This species has been recovering due to conservation efforts, leading to increased population densities in parts of its range.
- We used long-term data from three sites in the southeastern United States to determine if greater density led to more partial brood loss.
- We documented no evidence that density was linked to either early or late partial brood loss at any of the three sites, though we did show evidence that late partial brood loss may be increasing.
- These results indicate that other factors, including weather or habitat quality, may be more important than density in limiting this component of reproduction.

El aumento de la densidad asociado a la recuperación poblacional no explica la elevada pérdida parcial de la nidada en un reproductor cooperativo amenazado

RESUMEN

La pérdida parcial de la nidada en *Dryobates borealis*, un reproductor cooperativo amenazado a nivel federal en Estados Unidos, no estuvo asociada con aumentos en la densidad poblacional. En tres poblaciones —Sandhills, Carolina del Norte; Base del Cuerpo de Marines Camp Lejeune, Carolina del Norte; y Base de la Fuerza Aérea de Eglin, Florida— no encontramos evidencia que respalde efectos dependientes de la densidad sobre la pérdida parcial temprana o tardía de la nidada. Utilizando datos de monitoreo de nidos a largo plazo, evaluamos múltiples métricas del tamaño del grupo y de la densidad grupal en relación con la pérdida de la nidada en etapas tempranas (desde huevo a pichón hasta 6–10 días al momento del anillado) y tardías (desde el anillado hasta el volantón, hasta 38–40 días). Los resultados reproductivos no variaron con la densidad dentro de las poblaciones, lo que indica que el aumento reciente de la pérdida parcial de la nidada, particularmente hacia el final del período de pichones, no estuvo impulsado por un incremento en la densidad. Si bien tanto la densidad como la pérdida parcial de la nidada han aumentado con el tiempo, estas tendencias parecen estar desacopladas, lo que pone de relieve la necesidad de investigar otros posibles factores causales de la pérdida parcial de la nidada. La reproducción cooperativa puede amortiguar el rendimiento reproductivo frente a presiones relacionadas con la densidad mediante el cuidado parental compartido, pero a medida que las densidades aumentan debido a la recuperación poblacional impulsada por la conservación, los reproductores cooperativos pueden enfrentar restricciones nuevas o cambiantes. La variación en los resultados reproductivos puede estar más estrechamente vinculada a factores específicos del sitio o a presiones independientes de la densidad, como el clima, la depredación o la calidad del hábitat. A medida que las poblaciones de *D. borealis* continúan creciendo bajo los esfuerzos de recuperación en curso, comprender los mecanismos detrás de la pérdida parcial de la nidada sigue siendo fundamental para afinar las estrategias de conservación. Nuestros resultados se suman a la evidencia creciente de que los efectos dependientes de la densidad sobre la reproducción no son universales; el aumento de la densidad, aunque sea un éxito de conservación, no conduce necesariamente a una menor productividad ni a una mayor pérdida de nidadas.

Palabras clave: dependencia de la densidad, *Dryobates borealis*, éxito reproductivo, pérdida parcial de la nidada, reproducción cooperativa

INTRODUCTION

In birds, density-dependent mechanisms play a key role in population regulation, often leading to lower reproductive success and survival at higher densities (Dhondt et al. 1992, Both 1998, Sæther and Bakke 2000, Mallord et al. 2007). Shorter lifespans and faster life histories (e.g., earlier breeding, shorter reproductive windows; Martin 2004) may make temperate terrestrial bird species particularly sensitive to density-dependent constraints. Additionally, temperate regions experience strong seasonality, with resources like food and nesting sites being most abundant during the breeding season (Tökölyi et al. 2012, Watts et al. 2018). As population density increases, competition for these seasonal resources intensifies, potentially exacerbating the negative effects of density dependence on reproduction and survival.

The reproductive strategies of cooperatively breeding species contrast with those of most other temperate bird species. The social behaviors of cooperatively breeding species can help mitigate pressures on survival and reproduction, particularly those related to resource competition, predation, and environmental variability (Emlen 1997). Larger groups often achieve higher reproductive success by sharing parental care and territory defense (Brown 1987). More specifically, group members, also called “helpers” may increase overall provisioning at the nest (Dyer 1983, Emlen and Wrege 1991, Heinsohn 1992, Legge 2000, Brouwer et al. 2006). Cooperative breeding can also confer enhanced protection from nest predators, superior territory defense (Woolfenden and Fitzpatrick 1984), and improved adult survivorship (Ekman and Griesser 2016, Kerr et al. 2024).

At the same time, cooperative breeding may have costs. Individuals delay dispersal and reproduction to remain as helpers, and reproductive suppression of subordinates and skewed breeder success may occur within cooperative groups. Moreover, group living can result in competition over resources or increased disease (Koenig and Dickinson 2016) and parasite exposure (Cockburn 1998, Koenig and Dickinson 2016). Thus, while cooperative breeding can enhance reproductive success through social support, it also reflects a complex balance of costs and benefits that distinguish it fundamentally from the strategies of most other bird species.

Dryobates borealis (Red-cockaded Woodpecker) is a cooperatively breeding species that serves as a case study for understanding how population density affects nestling survival in cooperatively breeding birds over time. Found in longleaf pine (*Pinus palustris*), as well as other southern pine ecosystems around the edges of the range stretching across the southeastern United States, *D. borealis* lives in groups consisting of a breeding pair and 0–6 nonbreeding adult helpers. Each group occupies a cluster—a set of cavity trees used for roosting and nesting—within a defended territory. Group size in *D. borealis* is a strong predictor of productivity (Lennartz et al. 1987, Walters et. al 2016, DeMay et al. 2019). In recent years, *D. borealis* recovery efforts have primarily focused on increasing populations within their existing range, with only limited activities, such as translocations, aimed at expanding the species' range (Walters et al. 2002, U.S. Fish and Wildlife Service 2020). Key conservation strategies, including habitat restoration, artificial cavity creation, and improving habitat quality through frequent prescribed fire, have contributed to higher population densities and larger group sizes (Walters 1991, Walters et al. 2002, Martin et al. 2021). Given that recovery efforts often involve creating cavities near existing groups, these practices have led to *D. borealis* densities that are higher than those observed in the 1960s–1980s, prior to the implementation of intensive recovery efforts. At elevated densities, individuals may allocate more time and energy to territorial defense due to increased competition for space and resources, potentially reducing foraging efficiency and time allocated to reproduction (Garabedian et al. 2018). Garabedian et al. (2018) documented density-dependent reductions in clutch size and fledging success in *D. borealis*, highlighting how elevated density can negatively affect reproductive output.

Dryobates borealis populations are experiencing increased rates of partial brood loss (Garcia 2014), but the causes of this change are unknown. Partial brood loss is higher in *D. borealis* compared to other species of primary cavity nesters in the United States (LaBranche and Walters 1994). Most partial brood loss in *D. borealis* occurs early in the nesting period, with early partial brood loss resulting from a combination of partial hatching and nestling mortality in the first few days after hatching (LaBranche and Walters 1994, DeLotelle et al. 2004). Notably, 90% of nestling loss during the first week occurs within 2 days of hatching (Sanders 2000). In contrast, late partial brood loss results from nestling mortality alone during the latter half of the nestling period. Although early losses dominate overall patterns related to partial brood loss, our findings indicate that late partial brood loss may be increasing—a pattern not previously documented in the published literature. Anecdotal observations and published research have indicated declines in productivity in the southwestern portion of *D. borealis* range (Demay et al. 2019) and it is possible that those declines may be driven by density-dependent effects similar to those observed in South Carolina (Garabedian et al. 2014, Garabedian et al. 2018). Understanding at what densities increases in early and late partial brood loss emerge remains an important question for both basic research and conservation efforts.

Here, we analyzed long-term data to examine 2 measures of density—group density (i.e., number of territories in an area) and group size (i.e., number of adults within a group)—over time in 3 intensely studied *D. borealis* populations to investigate the extent to which these density measures influence early and late partial brood loss in *D. borealis*. Given that higher population densities can increase competition for resources, alter foraging efficiency, and intensify territorial interactions (Walters 1991, Walters et al. 2002, Garabedian et al. 2018, Martin et al. 2021), and populations are experiencing increased rates of partial brood loss, we predicted that (1) increasing group density leads to heightened competition for space and resources and will be associated with higher occurrences of partial brood loss, and (2) larger group sizes (i.e., more individuals to assist with provisioning) and lower local densities will be associated with fewer occurrences of partial brood loss. By testing these predictions across multiple populations, we aimed to assess whether density-dependent effects influence reproductive success in recovered *D. borealis* populations. Understanding whether current conservation strategies have unintentionally contributed to density-related trade-offs in fitness, and at what densities these effects begin to emerge, will be essential for determining the maximum sustainable densities for *D. borealis* and guide future management decisions.

METHODS

We acquired banding, group composition, and reproduction data from 3 *D. borealis* populations: (1) an inland site in the North Carolina Sandhills (1980–2023; 813 potential breeding groups; hereafter Sandhills), (2) a site on the central coast of North Carolina at Marine Corps Base Camp Lejeune (1986–2022; 136 potential breeding groups; hereafter Lejeune), and (3) a Gulf Coast Florida panhandle site at Eglin Air Force Base (2006–2023; 533 potential breeding groups; hereafter Eglin; Figure 1). All 3 areas were managed under long-term conservation plans designed to create and maintain high-quality habitat for *D. borealis*, with the exception of some privately owned parcels within the Sandhills study area that are not formally managed for *D. borealis*. Briefly, monitoring is facilitated by the resin-coated cavities excavated in living pines characteristic of this species, which are highly conspicuous, and by the long-term stability of territories. All territories in the study areas were visited prior to each breeding season to determine whether they were occupied, indicated by the presence of at least one active cavity tree. Thereafter, cavities were inspected within each active territory every 7–11 days to detect and monitor reproductive attempts. At 5–10 days post hatching, nestlings were banded with a unique combination of color bands. Groups were followed post-fledging to determine the identity and sex (based on sexually dimorphic crown patches) of fledged young. Color-banded adults were identified to obtain group size and composition, and each individual was assigned a status (e.g., breeder, helper, or floater—i.e., individuals that have dispersed from their natal territories but have yet to find a new territory or group to join) based on behavioral observations and their age. Unbanded adults immigrating into the study areas were captured from their roost trees and color banded. Refer to Walters et al. (1988) for a more detailed description of data collection. We were only able to include years when complete data were available for all three sites; thus, the site-years included in the analysis were variable based on the year data collection started for each site, with each site being analyzed separately for this analysis.

To assess population density and its effects on early and late partial brood loss, we used 2 metrics: group density (measured via Thiessen polygon size) and adults per hectare as a measure of group size (Garabedian et al. 2018). We used Thiessen polygon size as a spatial proxy for group density, with smaller polygons interpreted as reflecting higher local density and larger polygons indicating lower density (Garabedian et al. 2018). For each potential breeding group, we used the *sf* package in R (Pebesma 2018) accessed through R v4.2.2 (R Core Team 2024) to generate Voronoi (Thiessen) polygons based on the UTM coordinates of each active cluster center. We used the same mean cluster center for each potential breeding group for each monitoring year. For 1 site in 2022 (Lejeune) and 2 sites in 2023 (Sandhills and Eglin), we had complete records of the cluster centers for every potential breeding group that was monitored over the extent of the study. Using these 2022 and 2023 centers, we calculated 800-m (200-ha) buffers around each centroid to approximate Thiessen polygons for each cluster by year, ensuring that each cluster was assigned a unique group ID based on proximity to its respective centroid (Garabedian et al. 2022). The Voronoi tessellation split space equidistantly between neighboring centroids, resulting in smaller polygons when the number of groups in the area increased.

For each year and potential breeding group, we recorded the breeder male and male helpers, breeder female and female helpers, and floaters. We calculated group size as the sum of male and female breeders and helpers and excluded floaters. We divided the group size by the Thiessen polygon area to get the number of annual adults per hectare in each year.

For each potential breeding group, we included data on first nest attempts, clutch size, number of nestlings, and number of fledglings. We defined early partial brood loss as occurring during the incubation period (ranges from 11 to 14 days) to when the nestlings hatched and were banded at 6–10 days old. We defined late partial brood loss as occurring from the banding stage of the nestlings until they fledged at 38–40 days old. We counted eggs that did not hatch into nestlings and nestlings that died before banding as early partial brood loss. Nests with a single egg were excluded because it is not possible to distinguish between whole brood loss and partial brood loss for 1-egg clutches. Nests with >5 eggs were also excluded, as they are uncommon and typically are produced by co-breeding females and thus likely have different hatching dynamics than regular nests. Additionally, nests in which no eggs hatched were categorized as whole brood loss and hence were not included in the analysis. For early partial brood loss, we set a binary indicator to 0 if all eggs hatched and all nestlings were banded, and 1 if otherwise. Because our monitoring schedule did not allow us to distinguish between unhatched eggs and very early nestling deaths consistently, we treated both as part of early partial brood loss in analyses. Banded nestlings that did not fledge comprised late partial brood loss. We included only nests that produced at least 1 banded chick and at least 1 fledgling. For late partial brood loss, we set a binary indicator to 0 if all banded nestlings fledged, and 1 if otherwise. The sample size for early partial brood loss was larger than for late partial brood loss; late partial brood loss was a subset of the early partial brood loss dataset, including only those nests that had at least 2 chicks at banding (Supplementary Material Tables S1 and S2). We determined the clutch initiation date for each potential breeding group by using the age of the oldest nestling at banding to estimate the hatch date and subtracting 11 days (based on Ligon 1970) as the date the first egg was laid. We converted clutch initiation date to the ordinal date.

Statistical Analyses

We evaluated early and late partial brood loss separately for each of the 3 study sites. Covariates included the number of males (i.e., breeder males and male helpers), number of females (i.e., breeder females and female helpers), number of floaters, clutch size, lay date, group density (measured as the size of the Thiessen polygon), adults per hectare, and year. We assessed collinearity using Pearson's correlation coefficients and removed one of the pairwise variables if the absolute value of the correlation was >0.6. We checked for multicollinearity by examining the variance inflation factors (VIFs) for all variables. All variables with VIFs <10 were retained across all site-specific models to get our working global model (Supplementary Material Table S3; Dormann et al. 2013). At Lejeune, we observed strong correlation between the number of adults per hectare and the number of males with $r = 0.65$. The number of adults per hectare also exhibited a high VIF (>10). Therefore, we avoided including both predictors in the same model. We interpreted models with male count as capturing social group structure and those with the number of adults per hectare as capturing breeder density, allowing us to maintain biological clarity while minimizing collinearity concerns.

We built 62 unique models to determine the relative effect of density metrics, group density, and adults per hectare on the probability of occurrence of either early or late partial brood loss across all three sites. Each response variable was modeled as a logistic mixed-effects model using the *glmmTMB* R package (Brooks et al. 2017, R Core Team 2024). We constructed a priori models to include year and cluster ID as random effects and lay date as a fixed effect (Table 1). Then, we added different combinations of other covariates to create the model set. We ranked models using Akaike Information Criterion corrected for small sample size (AIC_c) and

ΔAIC_c (Akaike 1998, Supplementary Material Table S4) and performed model averaging for models with a $\Delta AIC_c \leq 2$. We classified predictors as significant if their estimated 95% model-averaged confidence intervals did not overlap zero. We present the significant model-averaged predictors from each a priori model for early and late partial brood loss at each site (Figures 2 and 3).

RESULTS

Group density increased (i.e., Thiessen polygon size decreased, Figure 4A) over time at Sandhills, reflecting a large increase in the number of groups within a study area of constant size. However, trends in group density were decreasing (i.e., Thiessen polygon size increased; Figure 4B, C) at Lejeune and Eglin. Although these study areas were also constant in size, population growth occurred largely by establishing new groups in unoccupied areas of what were initially spare and unevenly distributed. The number of adults per hectare increased at Sandhills, declined at Eglin, and showed an initial increase followed by a plateau at Lejeune (Figure 5). The occurrence of early partial brood loss at Sandhills and Eglin showed non-linear trends over time. At Sandhills, early partial brood loss declined from the late 1980s through the early 2000s but increased thereafter. At Eglin, the trend was relatively stable, with some evidence of an increase in more recent years. The occurrence of late partial brood loss increased at both Sandhills and Eglin, whereas early and late partial brood loss showed less consistent trends at Lejeune (Figures 6 and 7).

We tested for predictors of early partial brood loss at Sandhills (n = 2,274 cluster-years, where a cluster-year represents one breeding group (cluster) observed in a single year), Lejeune (n = 1,502), and Eglin (n = 513), and late partial brood loss at Sandhills (n = 1,903), Lejeune (n = 1,238), and Eglin (n = 370). Early partial brood loss models that included lay date received support for one of three sites while male count and clutch size received support for all 3 sites (Figure 2). Late partial brood loss models that included female count received support for one of three sites, lay date received support for one of three sites, year received support for one of three sites, and clutch size received support for two of three sites (Figure 3). Model-averaged parameter estimates provided no evidence that the 2 measures of density, group density and adults per hectare, were related to early or late partial brood loss.

Model-averaged parameter estimates for early partial brood loss indicated that as clutch size increased, the probability of early partial brood loss increased at Sandhills (1.02 ± 0.06, mean ± SE), Lejeune (1.18 ± 0.08, mean ± SE) and Eglin (1.08 ± 0.13, mean ± SE). As lay date progressed, the probability of early partial brood loss increased at Sandhills (0.38 ± 0.05, mean ± SE), and as the number of males in the group increased the probability of early partial brood loss decreased at Sandhills (–0.52 ± 0.05, mean ± SE), decreased at Lejeune (–0.45 ± 0.07, mean ± SE), and decreased at Eglin (–0.43 ± 0.11 mean ± SE; Supplementary Material Table S5).

Model-averaged parameter estimates for late partial brood loss indicated that the probability of occurrence of late partial brood loss increased as clutch size increased at Sandhills (0.24 ± 0.05, mean ± SE) and Lejeune (0.25 ± 0.06, mean ± SE). From 1980-2023, the probability of occurrence of late partial brood loss increased at Sandhills (0.29 ± 0.07, mean ± SE), and the probability of occurrence of late partial brood loss increased for later lay dates at Sandhills (0.34 ± 0.05, mean ± SE; Supplementary Material Table S5). As the number of females in a group increased, the probability of late partial brood loss decreased at Eglin (–0.25 ± 0.11, mean ± SE).

DISCUSSION

Both measures of density—group density and the number of adults per hectare – were unrelated to both early and late partial brood loss at all three study sites, indicating that partial brood loss in *D. borealis* is not affected by the number of neighboring groups or overall population density. This finding may result from the cooperative breeding system of *D. borealis*. In non-cooperative species, increased density often intensifies competition for resources or nest sites, leading to reduced reproductive success, but the social structure of cooperative breeders may mitigate these effects by distributing care among multiple group members. Alternatively, this lack of relationship between population density and partial brood loss may be because *D. borealis* densities at our sites were below the threshold at which density-dependent effects emerge. Previous studies (e.g., Garabedian et al. 2018) have shown that negative effects of density on productivity are evident in *D. borealis* at a particular density. Carrying capacity of our study populations is unknown, though 2 of the sites have now reached their recovery goals (within their original geographic extent). It may be that these populations remain well below carrying capacity, and that density-dependent processes could become more apparent as populations approach local carrying capacity. If this is the case, the densities for which *D. borealis* are currently managed (U.S. Fish and Wildlife Service 2003) may be well below what landscapes can support.

The probability of early partial brood loss increased in nests with larger clutches and later lay dates, indicating that early-stage brood reduction may be linked to reproductive investment and limited group support. Although late partial brood loss also increased with clutch size at some sites, there was a less consistent relationship with group composition (i.e., number of males and females) or lay date. Notably, late partial brood loss increased over time at one site, whereas early partial brood loss did not increase over time, indicating possible long-term shifts in late-stage reproductive outcomes.

The consistent effect of clutch size on early partial brood loss across all three sites indicates that laying more eggs does not necessarily lead to higher reproductive output. Instead, larger clutches appear to increase the probability of brood reduction, particularly during the early nestling period. This pattern supports the brood reduction hypothesis (Lack 1947), which posits that parents may overproduce offspring as a form of reproductive "optimism" in unpredictable environments. When resource availability or caregiving capacity is insufficient, some chicks may be lost—a cost potentially offset by the benefit of maximizing output under favorable conditions. This aligns with life-history and parental investment theory (Trivers 1996), which predicts trade-offs between offspring quantity and quality. In cooperative breeders, these trade-offs may be further shaped by the number and contribution of helpers (Hatchwell 1999). Although we did not directly measure group or helper investments in parental care, our findings indicate that social dynamics could impose additional constraints on clutch size, particularly if helper capacity is limited or if competition for resources reduces the group's ability to support larger broods (Emlen 1982, Koenig and Dickinson 2004). In our study, this influence of social dynamics appeared to be sex-specific: the number of adult males—but not overall group size—was negatively associated with reduced early partial brood loss. The negative association between the number of adult males and early partial brood loss suggests that helper effects in *D. borealis* depend more on the presence of specific helper types than on group size alone, with male helpers potentially mitigating the costs associated with larger clutches.

The effects of lay date on early and late partial brood loss at Sandhills indicate that *D. borealis* nests initiated later in the season are less successful, likely due to environmental or social constraints. Later nests typically yield lower reproductive success in temperate bird species, largely because late nests occur after the seasonal peak in food availability, resulting in poorer feeding conditions for chicks (Lack 1954, Perrins 1970, Verhulst and Nilsson 2008). In *D. borealis*, however, this pattern indicates that later nests may still succeed partially, but at a cost to total fledging output. This interpretation is supported by DeMay and Walters (2019), who reported that earlier nesting and larger group sizes predicted higher productivity across 19 *D. borealis* populations. Environmental factors known to influence breeding phenology—such as temperature, precipitation, and vegetation conditions—likely contribute to these outcomes. Warmer early spring temperatures are associated with earlier nesting and increased productivity, whereas more precipitation can delay breeding and reduce success (Fullerton et al. 2021). In addition, vegetation characteristics such as the presence of large pines and reduced hardwood midstory are linked to lower rates of partial brood loss, likely by improving foraging conditions prior to breeding (Martin et al. 2023).

The negative relationship between early partial brood loss and the number of males at all three sites supports long-standing evidence that larger social groups improve reproductive outcomes in cooperatively breeding species (Brown 1987, Emlen 1997). In *D. borealis*, group size is a consistent predictor of reproductive success, with larger groups associated with increased fledgling production and nest survival (Lennartz et al. 1987, Walters et. al 2016, DeMay et al. 2019, Kappes et al. 2020). These benefits align with broader patterns in cooperative breeders, where helpers contribute to provisioning, defense, and cavity maintenance (Lloyd et al. 2009, Preston et al. 2016, Van de Loock 2017). Our findings—that early partial brood loss is reduced in groups with more males—likely reflect the enhanced caregiving capacity provided by larger, male-rich groups.

In *D. borealis*, the reproductive benefits typically attributed to larger groups are largely driven by the presence of male helpers, which play a critical role in nestling care through food provisioning, cavity maintenance, and predator defense. Groups with one or more male helpers consistently fledge more offspring than those without (Khan and Walters 2002), underscoring that it is not only group size but also group composition that shapes reproductive outcomes. Helpers can have additive effects on nesting success by increasing the amount of food delivered to nestlings (Komdeur 1994, Doerr and Doerr 2007), especially in species prone to nestling starvation and brood reduction (Hatchwell 1999, Koenig and Walters 2011). In *D. borealis*, however, evidence for such effects is mixed: although helpers contribute substantially to provisioning (Khan and Walters 2002), their presence does not always translate to higher fledging success (Conner et al. 2004, Walters et al. 2016). We documented that the number of male helpers—rather than overall group size—was associated with reduced early partial brood loss, indicating that male helpers may alleviate the energetic demands placed on breeders by sharing foraging and defense duties. Such contributions may allow breeding males to allocate more energy to offspring care and future reproduction (Heppell et al. 1994, Walters 1990).

Female helpers led to reduced late partial brood loss at only one site in our study, contrasting with findings by Kerr et al. (2024), who did not detect an effect of female helpers on partial brood loss. This discrepancy may stem from differences in how brood loss was measured; Kerr et al. (2024) combined early and late partial brood loss, potentially obscuring effects that emerge later in the nestling period, when female helper contributions may become more influential, and looked at the amount of partial brood loss rather than whether or not it occurred. Additionally, female helpers make up a much larger proportion of the helper pool at Eglin—

where we observed this effect—indicating that demographic variation across sites may shape helper impacts.

Site-specific variation in the year effect on late partial brood loss among Sandhills, Lejeune, and Eglin indicates that temporal drivers of reproductive success—such as climate—may be more influential in some regions than others. Weather variability, including fluctuations in temperature and precipitation, can influence both nest initiation and partial brood loss in *D. borealis*. Interannual climate variation has been shown to affect nest initiation dates and overall reproductive success, highlighting the role of climate in shaping breeding outcomes (Fullerton et al. 2021). García (2014) similarly reported that partial brood loss increased over time at Sandhills and linked this pattern to increasing climate variability. Our findings refine this result by showing that the rise in partial brood loss at Sandhills is driven primarily by late partial brood loss, which was formerly rare, and that this trend appears confined to the inland population where climate variability—and ongoing climate change—are more pronounced. Notably, Sandhills is characterized by higher reproductive output but lower adult survival compared to the coastal Lejeune and Eglin sites, indicating that reproductive effort may be higher at Sandhills, potentially making reproduction more sensitive to climate variability at this site.

Future research that considers temporal and site-specific factors influencing reproductive success will advance knowledge about the drivers of partial brood loss in *D. borealis*. Our analyses used a binary indicator of brood loss. While this binary approach minimized the risk of overinterpreting imprecise estimates, examining the proportion of offspring lost remains a valuable direction that could help clarify mechanisms of brood reduction. Future work incorporating more frequent monitoring could also help disentangle the proximate drivers of early losses. Beyond this, the interaction between group density and habitat quality—such as cavity availability, food abundance, or vegetation structure—may play a critical role in shaping reproductive outcomes. Habitat quality can mediate the effects of social factors like density by influencing the resources available to breeding groups, their space use, and their ability to provision offspring (Conner et al. 1999, Garabedian et al. 2018). Notably, the highest density areas—at least at Sandhills and Lejeune—also correspond to the areas of highest habitat quality (Walters, unpublished data), indicating that increased density does not necessarily imply reduced resource availability. Additionally, long-term changes in climate (e.g., temperature and rainfall patterns) or site-level disturbances (e.g., fire frequency, timber harvest) could affect lay dates and resource availability, further shaping patterns of reproductive success. Incorporating habitat quality and environmental variability into future studies may reveal context-dependent effects of density that were not detectable in the present analysis.

Supplementary material

Supplementary material is available at *Ornithological Applications* online.

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Ethics statement

All research activities were conducted in accordance with applicable governmental regulations and institutional animal care and use guidelines. Fieldwork and data collection protocols were approved by the North Carolina State University Institutional Animal Care and Use Committee (IACUC Protocol ID: 21-206) and conducted under valid federal and state permits, including a Federal Bird Banding Permit (Permit No. 23311) and a Native Endangered Species Recovery—E Wildlife Permit (Permit No. ES087191). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Conflict of interest statement

The authors have no conflicts of interest to declare that are relevant to the content of this article.

Author contributions

Lauren D. Pharr and Caren B. Cooper conceived the study. Lauren D. Pharr, Caren B. Cooper, and Jeffrey R. Walters developed and designed the methods. Material preparation and data collection was performed by Lauren D. Pharr, and analysis was performed by Lauren D. Pharr and Nathan J. Hostetter. The first draft of the manuscript was written by Lauren D. Pharr and substantially edited by Christopher E. Moorman. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data availability

All non-sensitive data and analysis code are archived in Zenodo (DOI: https://doi.org/10.5281/zenodo.17835281). Sensitive location data for *Dryobates borealis* cannot be made publicly available due to federal restrictions and species protection concerns but may be shared with qualified researchers upon request and approval by the appropriate managing agencies.

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Table 1. Independent and dependent variables used in the development of a priori early and late partial brood loss occurrence models for each site. Variables are annotated as follows: (†) denotes a fixed and random variable and (§) denotes a random effect only. Variables in italics indicate inclusion in working global model where variance inflation factors were <10.

Variable	**Variable description**
Year †	Year
Cluster §	Cluster ID
Lay date	Estimated clutch initiation day
Clutch size	Number of eggs
Male count	Sum of breeder males and male helpers per cluster
Female count	Sum of breeder females and female helpers per cluster
Floater count	Total number of floaters per cluster
Total adults	Sum of breeder males, breeder females, male helpers, and female helpers
Group density	Total area (ha) per cluster
Adults per hectare	Total adults divided by total area (ha)

Figure 1. Location of the Sandhills (SH), Lejeune (LJ), and Eglin (EG) study sites where we monitored Red-Cockaded Woodpecker (*Dryobates borealis*) reproduction from 1980 to 2023 in the southeastern United States.

`[Alt Text]` Figure 1. Map of the southeastern United States displaying Red-cockaded Woodpecker (*Dryobates borealis*) nest monitoring sites. Three study sites are marked with asterisks and labeled: Sandhills in central North Carolina, Lejeune in eastern North Carolina, and Eglin in the western Florida Panhandle. A scale bar indicates a 3-mile reference, and a small inset map of the United States. in the lower right highlights the region shown. A compass rose at the top right shows north.

Figure 2. Model-averaged standardized coefficient plots for predictors influencing the occurrence of early partial brood loss for the Sandhills (**A**), Lejeune (**B**), and Eglin (**C**) study sites. Each plot displays estimated effects of multiple predictors—such as clutch size, year, and various interaction terms—on reproductive outcomes, with black points representing effect sizes and horizontal lines showing 95% confidence intervals. A vertical dashed line at zero indicates the null effect threshold.

`[Alt Text]` Figure 2. This figure presents model-averaged coefficient plots for three study sites: (A) Sandhills, (B) Lejeune, and (C) Eglin. Each plot displays estimated effects of multiple predictors—such as clutch size, year, and various interaction terms—on reproductive outcomes, with black points representing effect sizes and horizontal lines showing 95% confidence intervals. A vertical dashed line at zero indicates the null effect threshold. In panel A (Sandhills), several predictors, including interaction terms, exhibit notable effect sizes with relatively narrow confidence intervals, indicating stronger support. Panel B (Lejeune) features similar variables, though most confidence intervals overlap zero, indicating greater uncertainty. Panel C (Eglin) includes fewer predictors with wider intervals, reflecting lower precision and less conclusive effects. These plots collectively illustrate how the strength and uncertainty of predictor effects vary across sites.

Figure 3. Model-averaged standardized coefficient plots for predictors influencing the occurrence of late partial brood loss for the Sandhills (**A**), Lejeune (**B**), and Eglin (**C**) study sites. Each plot displays estimated effects of multiple predictors—such as clutch size, year, and various interaction terms—on reproductive outcomes, with black points representing effect sizes and horizontal lines showing 95% confidence intervals. A vertical dashed line at zero indicates the null effect threshold.

`[Alt Text]` Figure 3. This figure displays model-averaged coefficient plots for three study sites—(A) Sandhills, (B) Lejeune, and (C) Eglin—illustrating the estimated effects of various ecological and reproductive predictors on a response variable, along with their associated 95% confidence intervals. Each subplot presents individual predictors on the y-axis and effect sizes on the x-axis, where solid dots represent model-averaged estimates and horizontal lines indicate confidence intervals. A vertical dashed line at zero marks the threshold of no effect. Panel A (Sandhills) shows several predictors—including interaction terms such as Male Count × Year — with confidence intervals that do not cross zero, indicating stronger influence. In Panel B (Lejeune), although most estimates are clustered around zero, some predictors like Floater Count exhibit more substantial effects. Panel C (Eglin) includes a smaller number of predictors with generally wider confidence intervals, indicating greater uncertainty. Collectively, the plots compare the direction, strength, and certainty of predictor effects across study sites.

Figure 4. Temporal trends for group density (i.e., Thiessen polygon size) for the Sandhills (**A**), Lejeune (**B**), and Eglin (**C**) study sites. The x-axis represents Year, and the y-axis represents Average group density (ha) with different ranges tailored to each site.

`[Alt Text]` Figure 4. A panel of three-line graphs showing average group density (ha) over time at three study sites: (A) Sandhills, (B) Lejeune, and (C) Eglin. Each graph includes a black line with dots representing annual values and a dashed gray LOESS trendline illustrating the overall trend. Panel A (Sandhills) spans from ~1980 to 2023 and shows a decline in group density over time with high year-to-year variability. Panel B (Lejeune) covers a similar range and shows an increasing trend in group density, especially after 2000. Panel C (Eglin) begins in the mid-1990s and shows a rising trend in group density through 2023.

Figure 5. Temporal trends for average adults per hectare (i.e., number of adults divided by Theissen polygon size) for the Sandhills (**A**), Lejeune (**B**), and Eglin (**C**) study sites.

`[Alt Text]` Figure 5. A panel of three-line graphs showing trends in average adults per hectare over time for three study sites: (A) Sandhills, (B) Lejeune, and (C) Eglin. Each plot contains black connected data points for annual values and a gray dashed LOESS line representing the smoothed trend. Panel A (Sandhills) starts in the mid-1990s and shows fluctuating values with a general decline in adults per hectare through 2023. Panel B (Lejeune) spans from around 1980 to 2022 and shows a strong upward trend, particularly in the early years, with continued increases over time. Panel C (Eglin) also spans from ~1980 to 2023 and shows a steady rise in adult density until around 2010, after which the values fluctuate. The y-axis is labeled “Average adults per hectare,” and all x-axes are labeled with years, tilted for readability. Each panel is labeled with bold site codes.

Figure 6. Temporal trends for the proportion of groups experiencing early partial brood loss for the Sandhills (A), Lejeune (B), and Eglin (C) study sites.

`[Alt Text]` Figure 6. A panel of three-line graphs depicting trends in the average proportion of early partial brood loss over time at three study sites: (A) Sandhills, (B) Lejeune, and (C) Eglin. Each graph includes black dots connected by lines to represent yearly values and a dashed gray LOESS trendline showing smoothed temporal patterns. Panel A (Sandhills) spans from ~1980 to 2023, showing high interannual variability with a general decline from earlier decades, followed by a flattening trend. Panel B (Lejeune) covers a similar time span and shows an initial decrease in early partial brood loss through the 2000s followed by a recent upward trend. Panel C (Eglin) begins in the mid-1990s and displays high variability without a strong long-term directional trend, though the LOESS curve indicates a mid-period dip followed by a slight increase toward the end. The y-axis is labeled "Average proportion of early partial brood loss " and the x-axis is labeled "Year", with tick labels rotated for readability. Each subplot is labeled with its respective site in bold (A, B, C).

Figure 7. Temporal trends for the proportion of groups experiencing late partial brood loss for the Sandhills (A), Lejeune (B), and Eglin (C) study sites.

`[Alt Text]` Figure 7. A panel of three-line graphs showing the average proportion of late partial brood loss over time at three study sites: (A) Sandhills, (B) Lejeune, and (C) Eglin. Each graph features black dots connected by lines to represent annual values, overlaid with a gray dashed LOESS curve indicating the smoothed trend. Panel A (Sandhills) shows data from ~1980 to 2023, with an overall increasing trend in late partial brood loss despite some early dips and high year-to-year variability. Panel B (Lejeune) also spans ~1980 to 2022, with early high variation and a relatively flat or slightly rising LOESS trendline toward the end. Panel C (Eglin) begins around 1995 and shows fluctuating late partial brood loss values over time, with the

LOESS trendline indicating a steady increase, especially from 2010 onward. The y-axis is labeled "Average proportion of late partial brood loss", and the x-axis is labeled "Year" with tick labels angled for clarity. Each subplot is marked with a bold letter and site code (A, B, C).

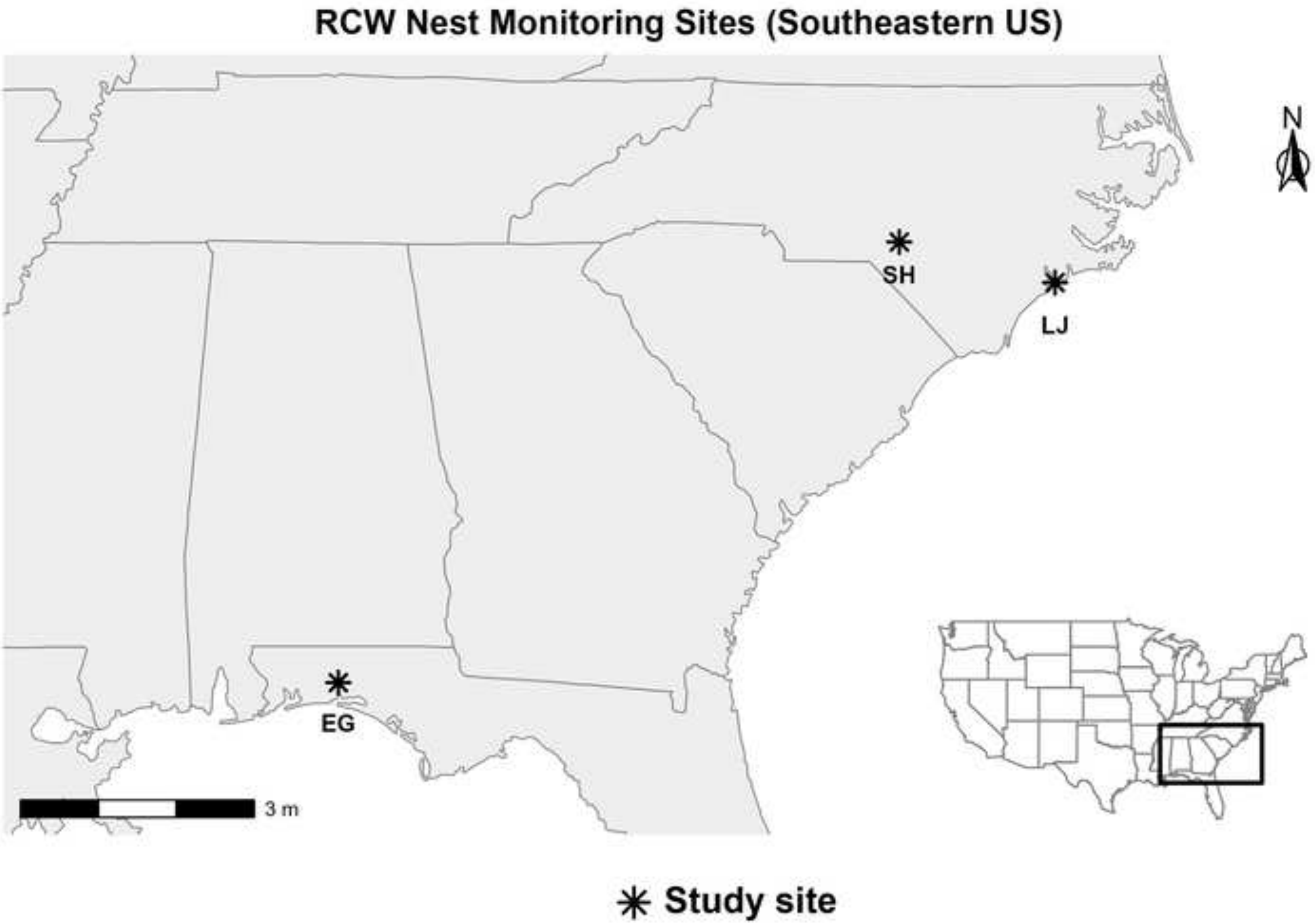
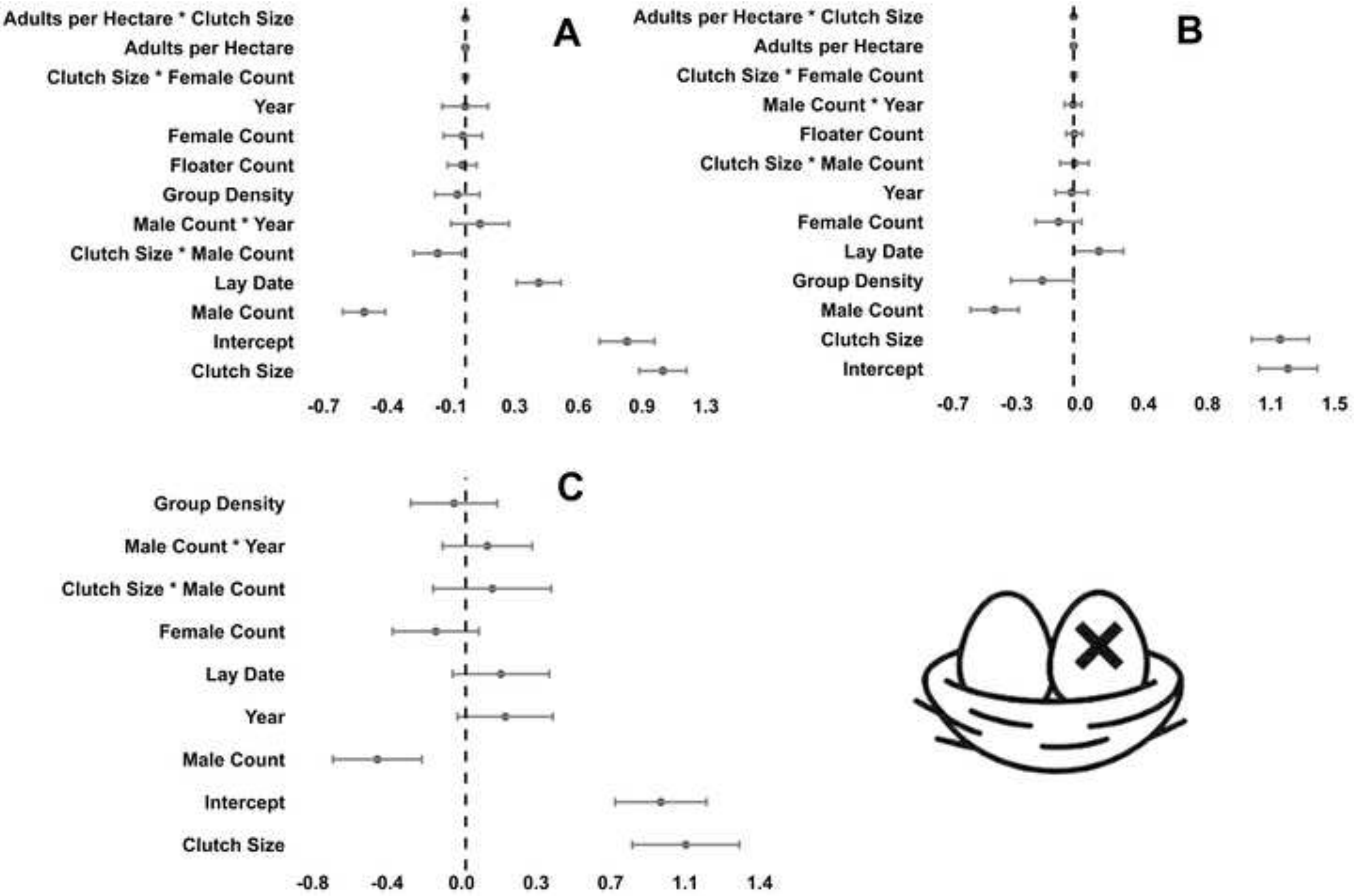

RCW Nest Monitoring Sites (Southeastern US)
N
SH
LJ
EG
3 m
✳ Study site

Figure 2


A
Adults per Hectare * Clutch Size
Adults per Hectare
Clutch Size * Female Count
Year
Female Count
Floater Count
Group Density
Male Count * Year
Clutch Size * Male Count
Lay Date
Male Count
Intercept
Clutch Size
-0.7
-0.4
-0.1
0.3
0.6
0.9
1.3
B
Adults per Hectare * Clutch Size
Adults per Hectare
Clutch Size * Female Count
Male Count * Year
Floater Count
Clutch Size * Male Count
Year
Female Count
Lay Date
Group Density
Male Count
Clutch Size
Intercept
-0.7
-0.3
0.0
0.4
0.8
1.1
1.5
C
Group Density
Male Count * Year
Clutch Size * Male Count
Female Count
Lay Date
Year
Male Count
Intercept
Clutch Size
-0.8
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0.0
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1.1
1.4

Figure 3

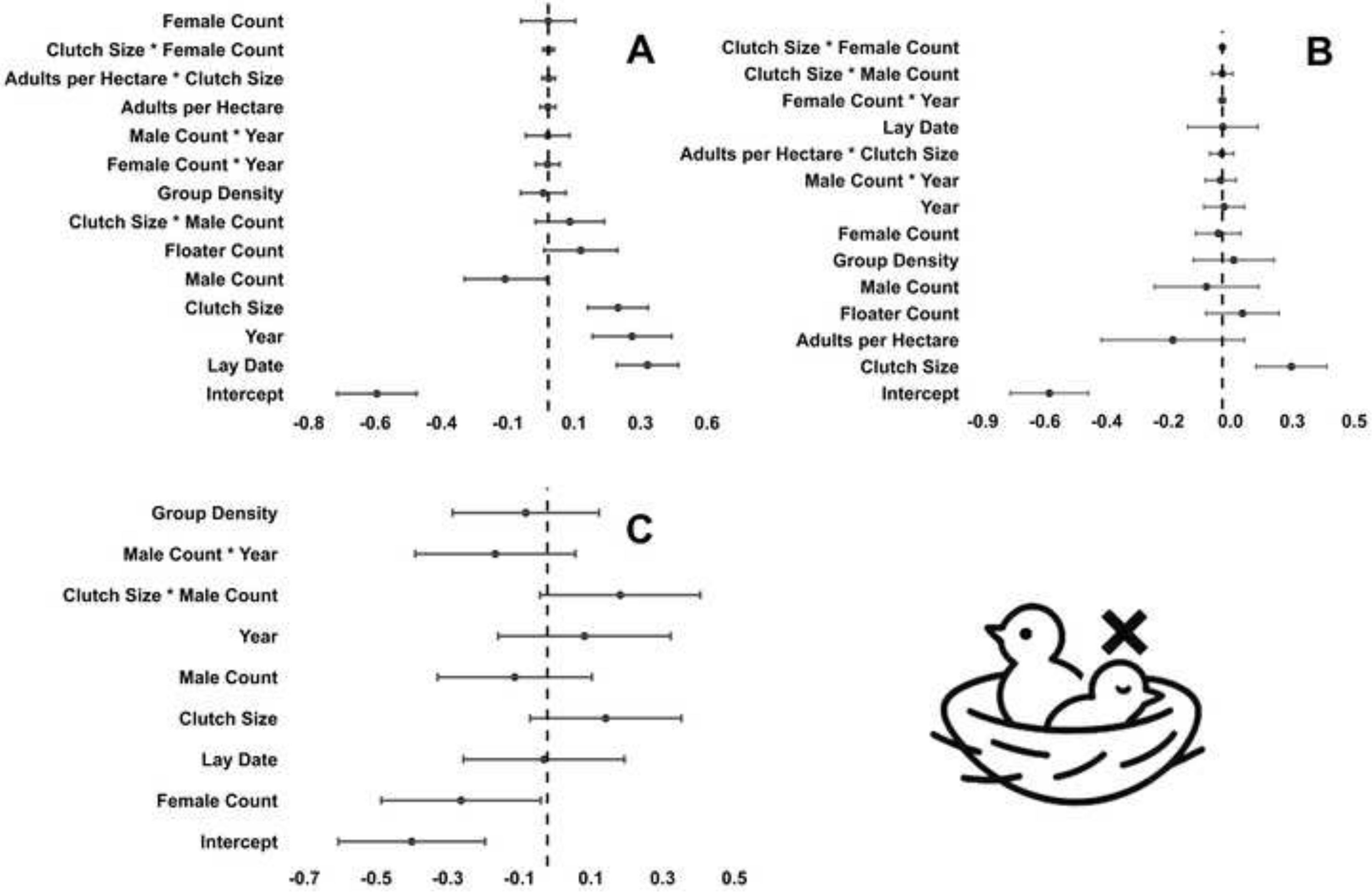
A
Female Count
Clutch Size * Female Count
Adults per Hectare * Clutch Size
Adults per Hectare
Male Count * Year
Female Count * Year
Group Density
Clutch Size * Male Count
Floater Count
Male Count
Clutch Size
Year
Lay Date
Intercept
-0.8
-0.6
-0.4
-0.1
0.1
0.3
0.6
B
Clutch Size * Female Count
Clutch Size * Male Count
Female Count * Year
Lay Date
Adults per Hectare * Clutch Size
Male Count * Year
Year
Female Count
Group Density
Male Count
Floater Count
Adults per Hectare
Clutch Size
Intercept
-0.9
-0.6
-0.4
-0.2
0.0
0.3
0.5
C
Group Density
Male Count * Year
Clutch Size * Male Count
Year
Male Count
Clutch Size
Lay Date
Female Count
Intercept
-0.7
-0.5
-0.3
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Figure 4

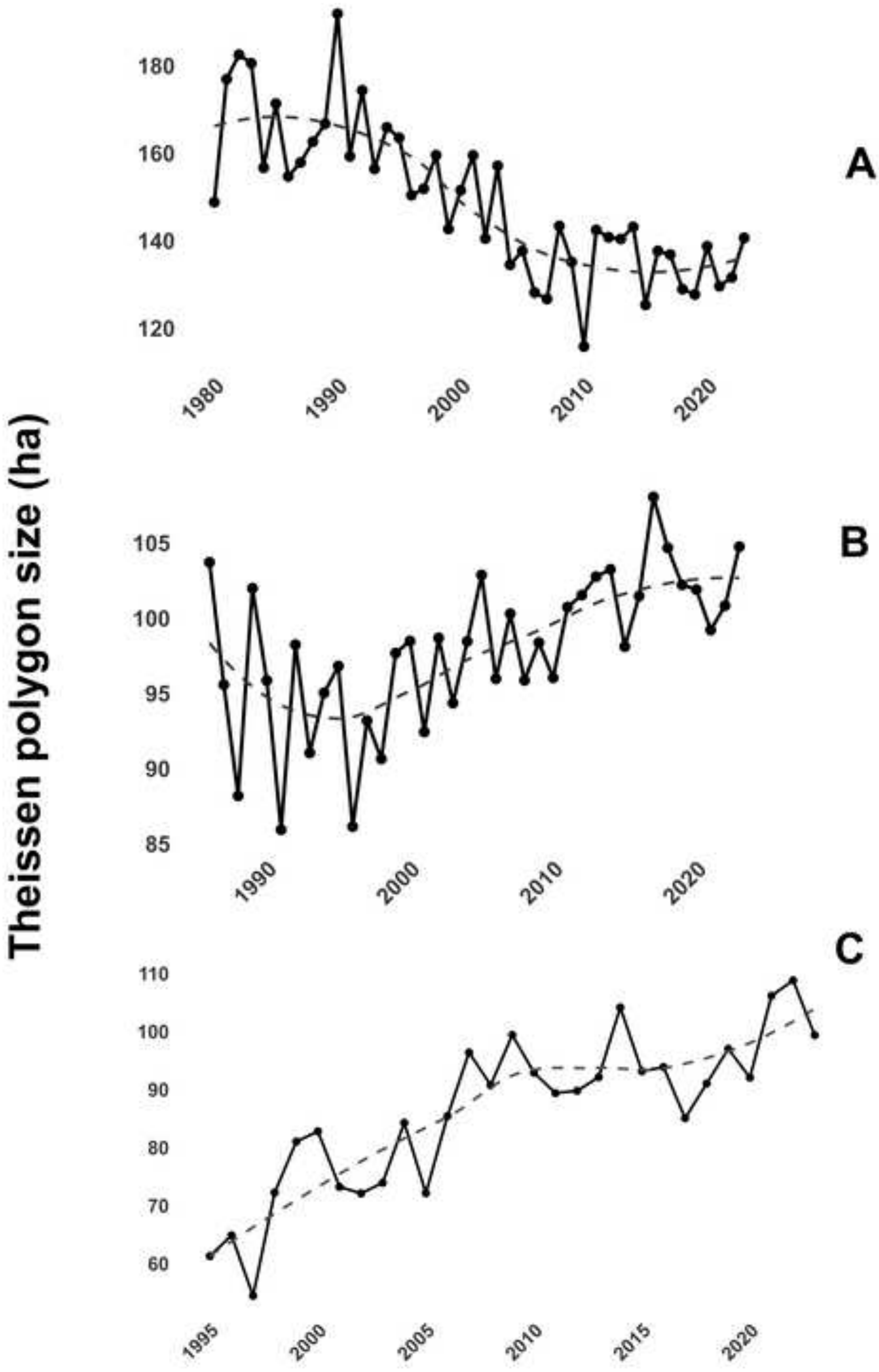
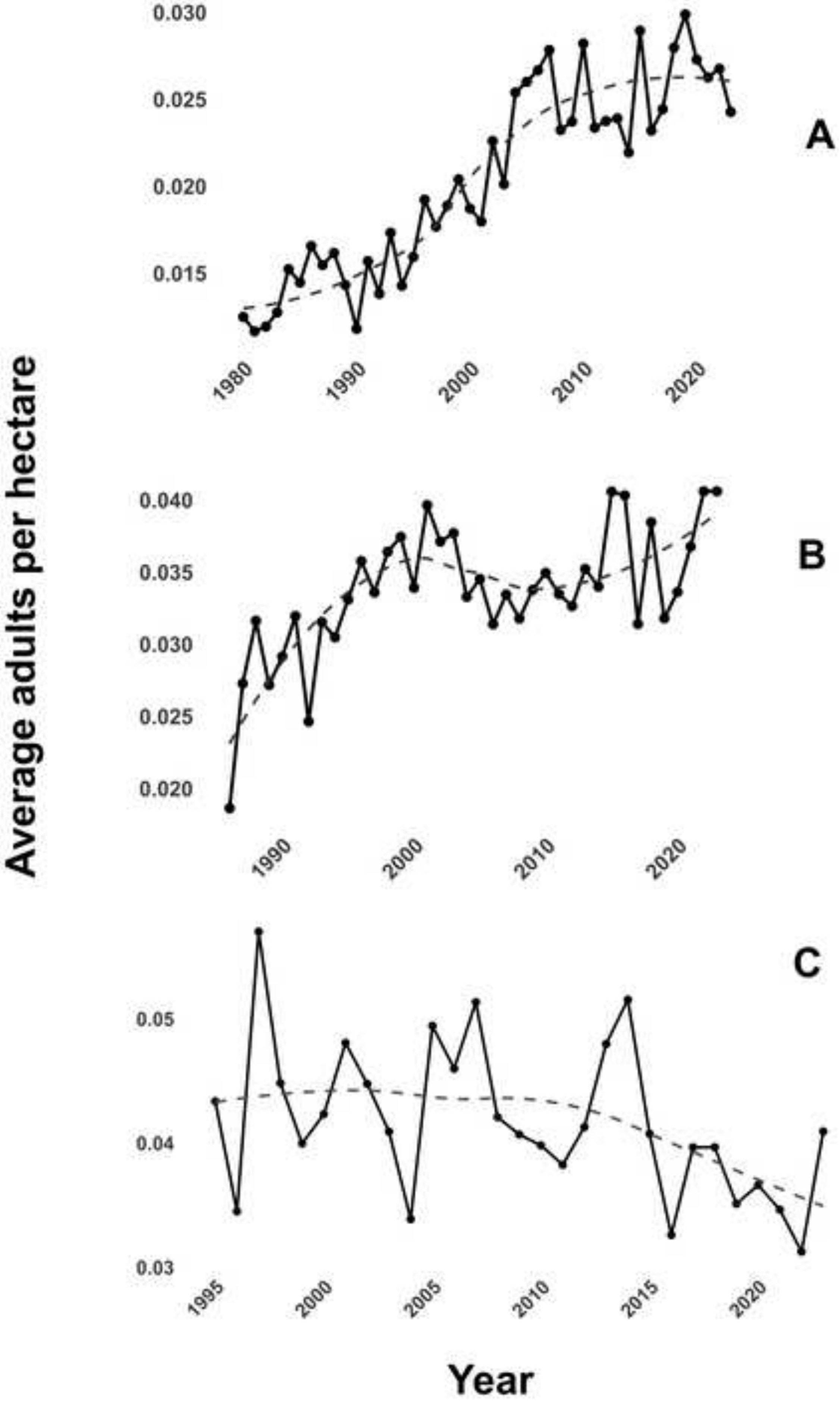

Theissen polygon size (ha)
A
180
160
140
120
1980
1990
2000
2010
2020
B
105
100
95
90
85
1990
2000
2010
2020
C
110
100
90
80
70
60
1995
2000
2005
2010
2015
2020

Figure 5


Average adults per hectare
A
0.030
0.025
0.020
0.015
1980
1990
2000
2010
2020
B
0.040
0.035
0.030
0.025
0.020
1990
2000
2010
2020
C
0.05
0.04
0.03
1995
2000
2005
2010
2015
2020
Year

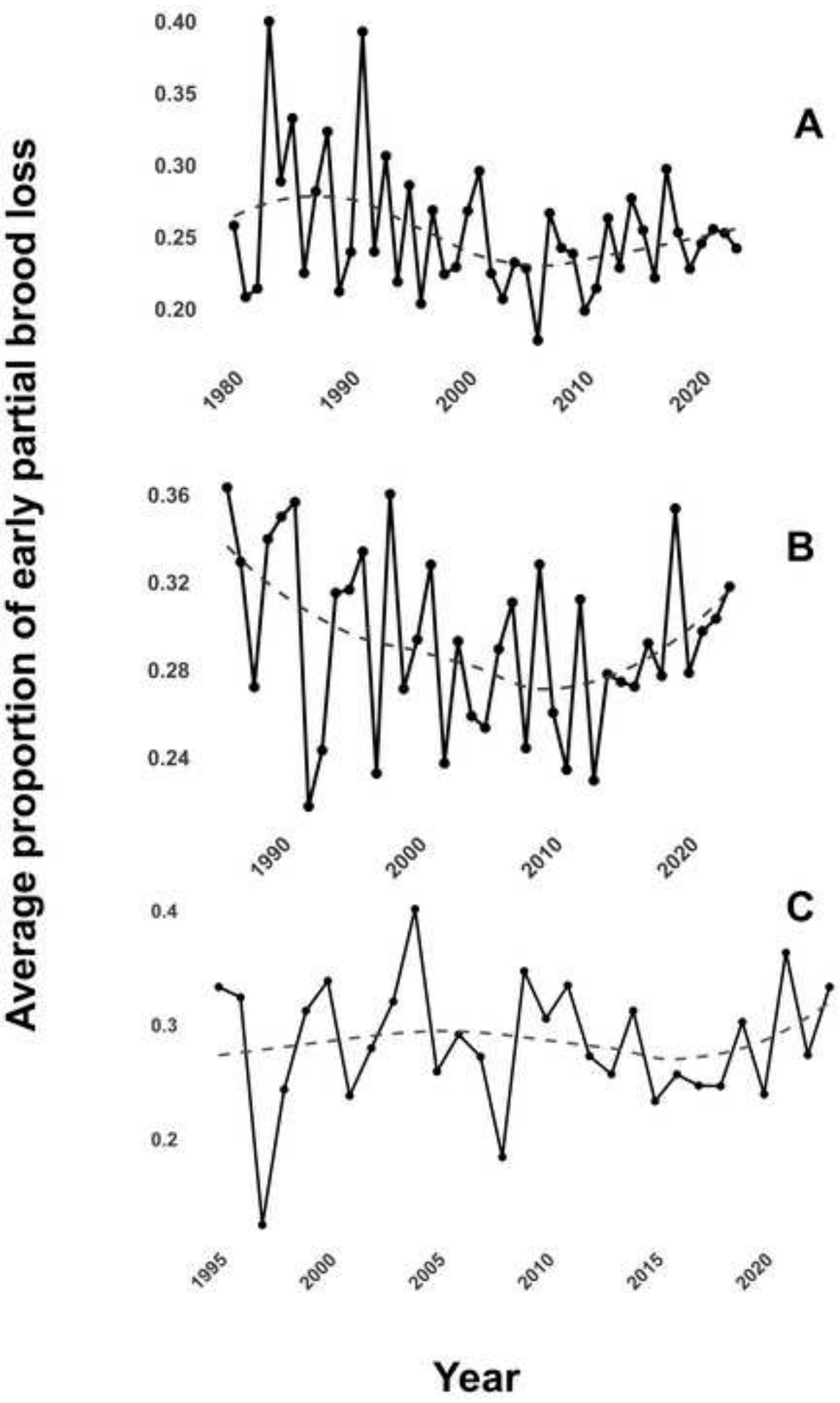
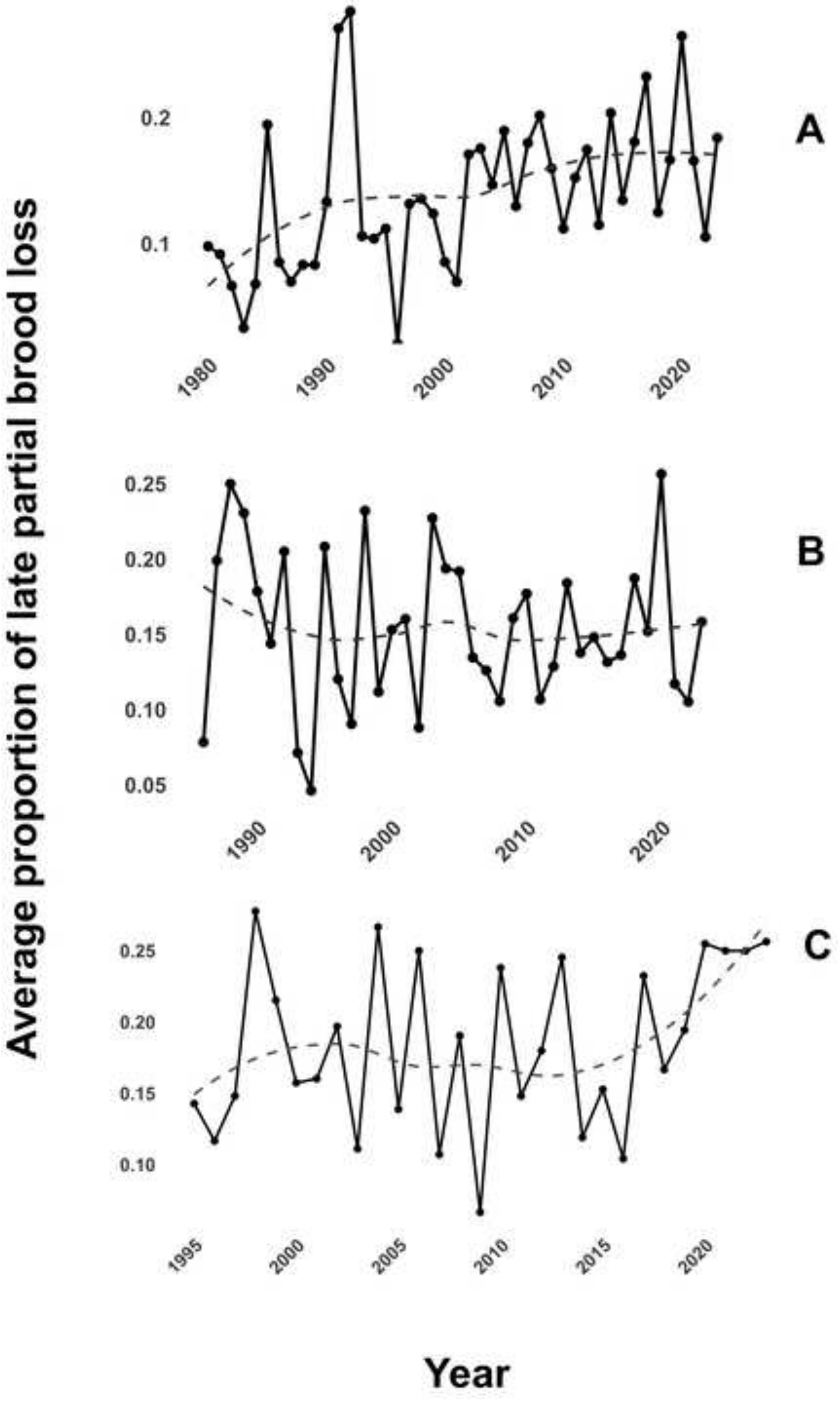

Average proportion of early partial brood loss
A
0.40
0.35
0.30
0.25
0.20
1980
1990
2000
2010
2020
B
0.36
0.32
0.28
0.24
1990
2000
2010
2020
C
0.4
0.3
0.2
1995
2000
2005
2010
2015
2020
Year

Figure 7



Average proportion of late partial brood loss
0.2
0.1
1980
1990
2000
2010
2020
A
0.25
0.20
0.15
0.10
0.05
1990
2000
2010
2020
B
0.25
0.20
0.15
0.10
1995
2000
2005
2010
2015
2020
C
Year