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EFFECTS OF CLIMATE CHANGE ON NORTHERN BOBWHITE NESTING CHRONOLOGY AND CLUTCH SIZE

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ABSTRACT

Widespread changes to breeding bird phenology in response to climate change have been apparent in North America for several decades. While the impact of an earlier breeding season may be minimal by itself, changes in community-level interactions can be greatly influenced because of varying responses to climate change in different trophic levels. Climate change has been shown to alter the onset of breeding season and chick survival, and lead to population declines for game birds in high latitudes, at high elevations, and on the periphery of their range. The topic of climate change in relation to northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) populations has attracted interest in the past 2 decades. Some researchers have hypothesized that climate change has the potential to cause the breeding season to initiate sooner and have a shorter duration. Using a 29-year dataset (1992–2020) with 1,171 individual bobwhites, we analyzed how temperatures prior to the breeding season affected the timing of nest initiation and clutch size, and how the length of the breeding season varied over time. We determined that the average minimum daily temperatures 30 days prior to the breeding season warmed by 0.07° C/year from 1992–2020. For any given year, we found that nest initiation could occur 1.12 days earlier for every 1° C increase in temperature. Overall, we determined that the timing of the nesting season had not changed from 1992–2020. The overall average breeding season length (135 days) or last average initiation date (27 Aug) did not change over the course of our study. We did not find that clutch sizes have changed over time and they were not correlated to pre-laying temperature. We attribute the lack of significant change in nesting chronology to plasticity of populations within the core of the range and the intensity of bobwhite management on the landscape.

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Key words: breeding phenology, *Colinus virginianus*, nest initiation, northern bobwhite, temperature

Climate change has the potential to adversely affect wildlife to the extent of threatening the population persistence of those that cannot adapt to adverse extrinsic environmental factors. Studies have demonstrated that climatic changes can affect avian distributions (Root 1988), migration patterns (Sparks 1999), reproductive output (Torti and Dunn 2005), and survival rates (Barbraud and Weimerskirch 2001). Researchers have suggested that animal populations in higher latitudes are much less stable as compared to low- or mid-latitude populations (Hampe and Petit 2005) in the face of climate change. Researchers of game bird species have documented changes in the breeding phenology of high latitude populations of black grouse (*Lyrurus tetrix*) in Finland (Ludwig et al. 2006) and red grouse (*Lagopus lagopus*) in Scotland (Fletcher et al. 2013) as a result of warming spring temperature prior to the onset of breeding. While populations at such latitudes may be at a heightened risk when challenged by warming temperatures, other research suggests that populations found in more southerly latitudes are actually more prone to extinction (Sinervo et al. 2010). Researchers suggest that species found in the lower and mid-latitudes may not have the ability to adapt quickly to climatic extremes given they are acclimated to more temperate weather conditions (Sheldon 2019).

The northern bobwhite (*Colinus virginianus*; hereafter, bobwhite), like other imperiled ground nesting species, is also potentially vulnerable to a changing climate, especially on the fringe of its range. The potential effect of climate change on bobwhite population persistence has importance beyond the conservation of a single species. Bobwhite serve as an umbrella

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species for other wildlife (Crosby et al. 2015) and lands that are conserved in the name of intensive bobwhite management have an immense economic impact on local economies (Burger et al. 1999, Fleckenstein 2020).

With bobwhite populations decreasing significantly over the last 60 years range-wide (Sauer et al. 2017), researchers and managers alike have hypothesized on potential causes of the decline. Outside of the relatively well understood issues that bobwhite are facing such as habitat loss, habitat fragmentation, and predation (Brennan 1991, Rollins and Carroll 2001), climate change effects on bobwhite populations are mostly unknown. To our knowledge, there have been no studies that have analyzed the relationship between bobwhite demographics and climate change using long-term empirical data. In studies conducted using short spans of data or data based on simulation modeling, researchers have suggested that there is the potential for shorter breeding seasons, reduced reproductive output, and altered ranges in some localities (Guthery et al. 2000, Lusk et al. 2001, Rolland et al. 2011). Most earlier studies have been conducted on the edge of the bobwhite range, where extreme weather events (e.g., drought, prolonged freezing weather, flooding) are much more likely to impact bobwhite demography. It is currently unknown how changing climatic conditions are affecting bobwhite populations in the core of their range. The topic has gained much attention as researchers have reiterated the need for studies on how climate could be affecting bobwhite populations and how potential impacts will influence future management decisions (Guthery 2000, Lusk et al. 2001, Rolland et al. 2011, Martin 2012, Hernández et al. 2013).

Researchers need long-term datasets to study how critical issues such as climate change may affect bobwhite and to help resource managers make informed decisions. Given researchers' growing concern about bobwhite and climate change over the last 2 decades, we wanted to determine whether a relationship existed between climate and bobwhite breeding ecology in low altitude and low latitude populations within the core of the bobwhite range. Our objectives were to analyze the effects of temperature on the timing and duration of the bobwhite nesting season and the resulting effect on clutch sizes and to determine whether any of these variables have changed over 3 decades in any biologically meaningful ways. We hypothesized that bobwhite breeding chronology or clutch size would not vary significantly over time. We predicted that because our study area was located within the core of the bobwhite range, climate variables were less likely to affect populations as compared to populations found on the periphery.

STUDY AREA

Our study was conducted on an 8,000-ha privately owned property in Baker County, Georgia, USA that has been intensively managed for bobwhite hunting since the mid-1900s. The site is among similarly managed properties in the Albany, Georgia area totaling approximately 100,000 ha within the core of the bobwhite range (i.e., centrally located within the historical bobwhite range). The property is primarily low basal area upland pine (60%) consisting mostly of slash pine (*Pinus elliottii*), longleaf pine (*P. palustris*), and loblolly pine (*P. taeda*) with occasional live oak (*Quercus virginiana*) hammocks (5%) interspersed, planted loblolly pine for timber production (10%), and few hardwood drains and wooded wetlands (5%) along the Flint River. Annually disked fallow fields (20%) are found throughout the uplands and primarily consist of common ragweed (*Ambrosia artemisiifolia*) and camphorweed (*Heterotheca subaxillaris*). Ground cover in the uplands is primarily forbs (e.g., *Chamaecrista nictitans, Desmodium* spp., *Lespedeza* spp.) and native warm-season grasses. A detailed description of this site can be found in Yates et al. (1995), Burger et al. (1998), Hughes et al. (2005), and Terhune et al. (2006). This site is 50 m above sea level, receives approximately 130 cm of rainfall annually, and has an average daily high temperature of 25.6° C and an average daily minimum temperature of 12.2° C. In the breeding season (i.e., Apr–Sep), the site receives approximately 69 cm of rainfall and has an average daily high temperature of 31° C and an average daily minimum temperature of 18.9° C.

METHODS

Bobwhite Metrics

Adult bobwhites were trapped twice per year (Oct–Nov and Feb–Mar) using baited funnel traps (Stoddard 1931) from 1992–2020. Individuals captured were aged, sexed, weighed, banded with aluminum leg bands, and released at the trap site. A subset of individuals that weighed ≥132 g were radio-tagged with 6.2 g pendulum-style transmitters equipped with an activity switch (Holohil Systems, Ltd., Carp, Ontario, Canada). Bobwhites were tracked ≥2 times/week during the breeding season (1 Apr–30 Sep) to locate nests and determine nest fate. Individuals located in the same location for consecutive days were assumed to be incubating. Incubating nests were visited daily to monitor nesting progress until they were determined to be successful or failed. When the radio-tagged bobwhite was not present at the nest, eggs were counted to determine clutch size. Nests that began incubation on or before 1 June were considered to be the first nesting attempt for that individual bird. We calculated the nest initiation date using (incubation date) – (1.2 × clutch size) (Klimstra and Roseberry 1975) for each nest as ordinal date (1 Jan = 1). The population-level first nesting attempt was defined as the average date of incubation for the first nesting attempts for all individuals, and the earliest nest initiation date was defined as the first attempt of any individual for that year.

Climate Data Variables

Historical climate data for the study were obtained (NOAA National Centers for Environmental Information 2021) for the Southwest Georgia Regional Airport in Albany, Georgia (~20 km from study site). Daily precipitation, minimum temperature, maximum temperature, and average daily temperature were collected for each day throughout the study period. Bobwhite hens begin increasing in weight approximately 1 month before producing eggs (Roseberry and Klimstra 1971). Therefore, we decided that the pre-laying temperature (PLT) that could affect the onset of incubation was 30 days before the onset of incubation. We used the average PLT for the 30-day pre-laying period of the first 5 years of the study as our baseline to determine whether temperatures were changing on our study area.

Analysis

We used linear regression to model the relationship between climate variables and year. We tested for serial correlation in the error terms using the "acf" function in R (R Version 1.3.1093, www.R-project.org, accessed 10 Feb. 2021) but no correlations were detected, negating the need for more complex error terms. We used generalized linear models to test the effect of climate variables on nest initiation and clutch size using the lme4 package (Bates et al. 2015). Year was treated as a random effect because multiple individuals were included per year. A Gaussian error term was used for the nest initiation models and a Poisson error term with a log link was used for the clutch size models. We used likelihood ratio tests to determine whether covariate models were more supported than the null model. For all models fitted, an alpha of <0.15 and 85% confidence limits were used to be able to detect change more liberally. We used marginal r^2 based on Nakagawa and Schielzeth (2013) to determine the amount of the variance explained by the fixed effect in the mixed effects models. Conventional r^2 was used for the simple linear regressions.

RESULTS

The average daily pre-laying temperature (PLT) was 19.8° C (SE = 0.06, range = 17.1–23.7) between 1992–2020 and showed no trend during the time series ($P = 0.28$, $df = 27$). The average maximum daily PLT was 27.0° C (SE = 0.06, range = 24.3–29.7) between 1992–2020 and also showed no trend ($P = 0.83$, $df = 27$). The average minimum daily PLT was 12.5° C (SE = 0.08, range: 8.6–17.7) between 1992–2020 and increased by 0.07° C/year ($P = 0.13$, $df = 27$, CI = 0.004–0.14; Figure 1). Average total precipitation 30 days prior to the onset of nest initiation was 7.6 cm (SE = 1.01, range = 1.27–21.08) and did not vary across years ($P = 0.35$, $df = 27$).

We collected nest data from 1,171 individual bobwhites from 1992–2020 that produced 1,598 total nesting attempts. We determined that 548 of those were considered first nesting attempts (i.e., nest initiation occurred on or before 1 Jun). The average population-level nest initiation date of first attempts across years was 8 May (day 127) (SE = 0.62, range of annual means: 26 Apr–18 May, day 115–137) and showed no trend ($P = 0.25$, $df = 27$) between 1992–2020 (Figure 2). The earliest nest initiation of the season did not vary across years ($\bar{x}$ = 14 Apr, SE = 0.51, $P = 0.185$, $df = 27$, range: 12 Mar–13 May).

According to the likelihood test, the pre-laying temperature model fit the data better than the null model ($\chi^2 = 3.95, df = 1, P = 0.05$). For every 1° C increase in the 30-day pre-laying temperature period, nest initiation occurred 1.12 days earlier ($P = 0.06$, $df = 26.2$, CI = –1.92 to –0.33; Figure 3); however, the model explained very little variation (marginal $r^2 = 0.01$). Precipitation 30 days prior to the nesting season was not shown to affect nest initiation timing ($P = 0.19$, $df = 27$). The average clutch size for all nests was 12.3 eggs (SE = 0.32, range = 2–29) while the clutch size of first attempt nests averaged 14.32 eggs (SE = 0.15, range = 4–29). Clutch size

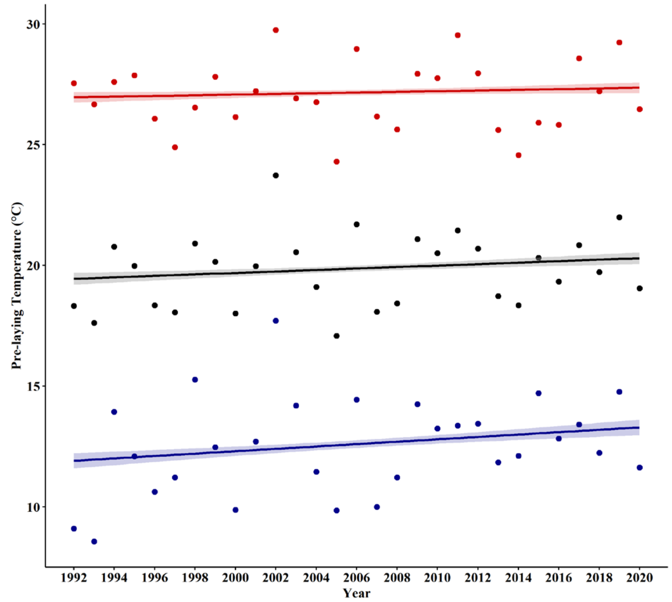

Fig.1. Average daily minimum (blue), mean (black), and maximum (red) pre-laying temperatures from 1992–2020 on privately owned property in Baker County, Georgia, USA and model predicted trendline with 85% credible intervals ($r^2 = 0.03$, $P = 0.28$).

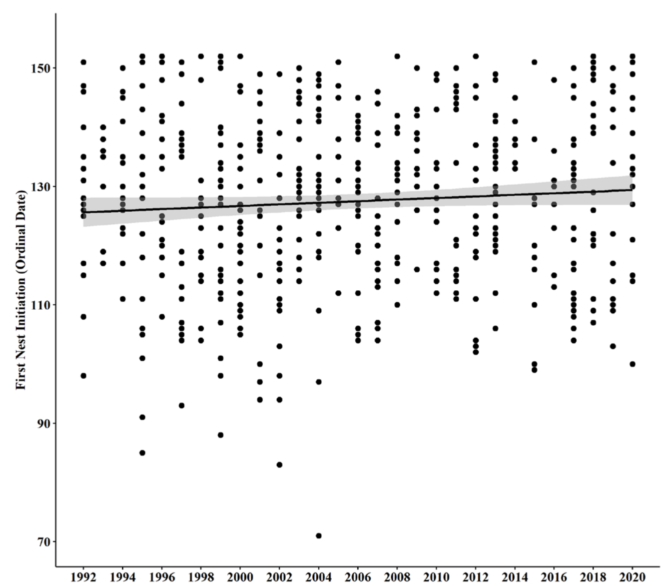

Fig. 2. Model-estimated mean nest initiation date from 1992–2020 and 85% credible intervals on a privately owned property in Baker County, Georgia, USA ($r^2 < 0.01$, $P = 0.25$).

did not vary by year ($P = 0.355$, $df = 27$) and was not affected by any climate variable (Figure 4). The average length of the nesting season (i.e., when nests were being initiated) was 135 days (SE = 3.11, range = 90–168) that lasted on average from 14 April–27 August (Figure 5). We detected no change in the last initiation date ($P = 0.18$, $df = 27$) or the overall nesting season length ($P = 0.957$, $df = 27$).

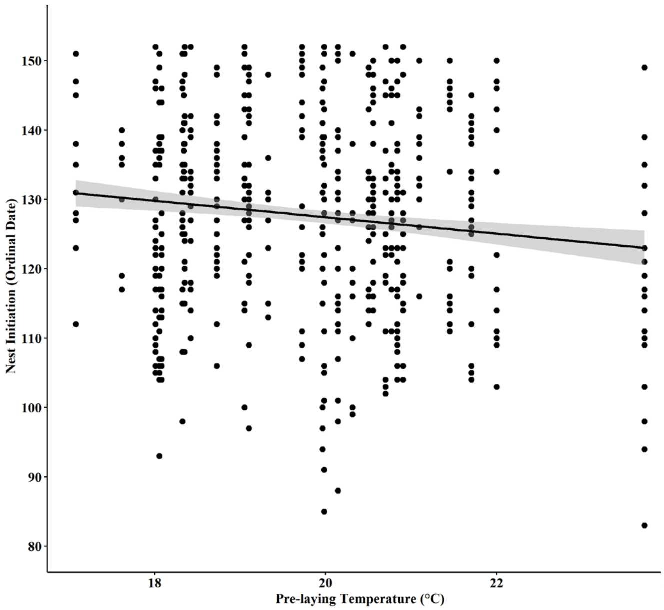

Fig. 3. Relationship between pre-laying temperatures collected and nest initiation dates of northern bobwhite (*Colinus virginianus*) from 1992–2020 on a privately owned property in Baker County, Georgia, USA and model-predicted trendline with 85% credible intervals ($r^2 = 0.01$, $P = 0.06$).

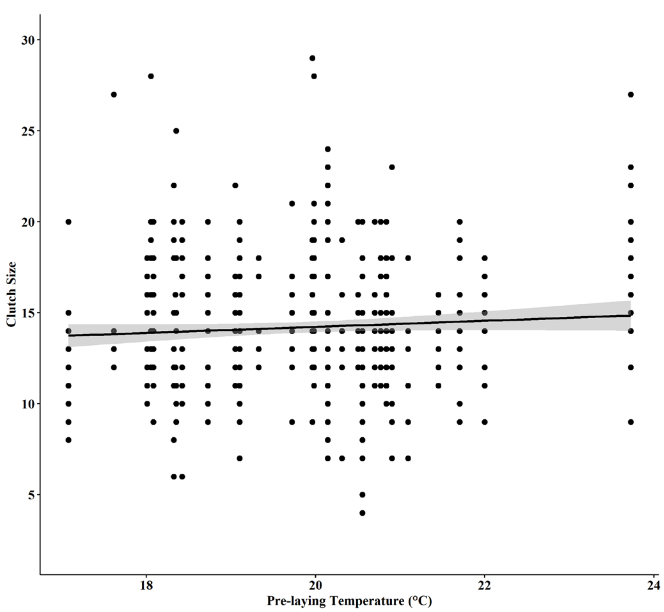

Fig. 4. Relationship between clutch sizes of first nesting attempts of northern bobwhite (*Colinus virginianus*) and pre-laying temperature from 1992–2020 on a privately owned property in Baker County, Georgia, USA and model-predicted trendline with 85% credible intervals ($r^2 < 0.01$, $P = 0.13$).

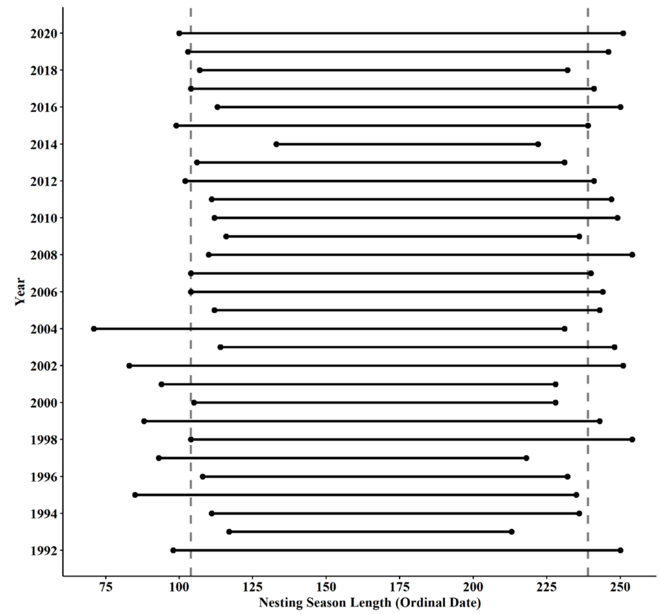

Fig. 5. Northern bobwhite (*Colinus virginianus*) nesting season length (displayed as ordinal dates, 75 = Mar 17, 250 = Sep 8, horizontal solid lines) and average start and end dates (vertical dashed lines) from 1992–2020 on a privately owned property in Baker County, Georgia, USA.

DISCUSSION

Our results suggest that while pre-laying temperatures have warmed slightly over the last 3 decades, a warming climate has not had a biologically meaningful influence on bobwhite nesting chronology or clutch size on our study area. While annual temperatures across the United States have averaged 0.75° C higher from 1992–2020 as compared to the preceding 97 years, temperatures in our study area have been only 0.46 °C higher across the same time period (NOAA National Centers for Environmental Information 2021). It is possible that climate during the spring and early summer months may be changing at a slower pace in southern latitudes and low elevation as compared to more northern latitudes and higher elevations (Flato and Boer 2001).

We found that clutch size did not vary according to any climatic factor and did not vary by year. This finding is consistent with other studies that found no link between temperatures and clutch size (Pendlebury and Bryant 2005, Fletcher et al. 2013). It is likely that other factors such as timing during the breeding season (Perrins and McCleery 1989), the number of nesting attempts (Aslan and Yavus 2010), or changes in food availability (Lack 1947) affect clutch size more than ambient temperature. The average clutch size during our study was 12.3 eggs. A study conducted on a nearby property from 1967–1971 concluded that average clutch size was 12.0 eggs (Simpson 1972). When we compare our 29-year dataset and data from Simpson (1972), it does not appear that clutch size has changed in Southwest Georgia over the last 50 years.

We documented that bobwhite nesting on our study area was minimally affected by temperature and nests were initiated 1.12 days earlier for every 1° C increase in the 30-day pre-laying period during the spring. Our results indicated that the window for the beginning of bobwhite nest initiation could vary by a week depending on the average daily temperature leading up to the breeding season. While photoperiod is the primary environmental cue for breeding chronology (Dawson 2008), seasonal temperatures can also dictate the onset of breeding (Brown et al. 1999, Dunn 2004, Fletcher et al. 2013). If temperatures in the period prior to the onset of breeding begin to increase incrementally on an annual basis, there is a potential for a consistently earlier breeding season in bobwhite. While a shift in the bobwhite breeding by itself may pose little risk to the population, there is potential for a mismatch between the peak of hatching and food resource availability (Dunn and Winkler 1999). A potentially earlier start to the breeding season could also reduce the window of allowable time for managers to conduct annual prescribed burns, mowing, and timber harvests. Nonetheless, the current influence of climate on nest initiation is minor.

We did not observe any change in the timing of bobwhite nest initiation from 1992–2020. This outcome is contrary to the findings of many researchers who have determined that some bird species, particularly in high altitudes and latitudes, are nesting earlier (Ludwig et al. 2006, Fletcher et al. 2013). The results of these studies align with other research that suggests that animals existing in high altitudes and latitudes are more vulnerable to climate change (Hampe and Petit 2005). The population we studied, which is found in the core of the range, appears to be insulated from any apparent changes at this time. The length of the breeding season was fairly consistent across years as 93% (27/29) of all years were within 1 standard deviation of the mean season length. Of the 2 years that fell outside of one standard deviation from mean, both were severe drought years. While there were several years prior to 2005 where the nesting season began noticeably earlier, these were individual nests and most nests thereafter began within the normal window of time.

Our results did not align with predictions from Guthery et al. (2000), who suggested that the bobwhite breeding season length would decline over time and lead to a slow annual rate of decline. This hypothesis is likely to be more applicable on the fringe of the bobwhite range where weather patterns are more extreme. Hampe and Petit (2005) also suggested that animals are more likely to exhibit change in response to climate at range margins. We have not seen evidence of this within the core of the range, where population density has actually increased by 0.12 bobwhite/ha/year over the duration of the study. Compared to bobwhites on the edge of their range, it is likely that populations within a landscape of intentional bobwhite management such as the one in our study may be buffered from modest climatic changes that have occurred so far. In addition, cultural practices such as supplemental feeding (Sisson et al. 2000, Buckley et al. 2015) and meso-mammal predator removal (Jackson et al. 2018, Palmer et al. 2019, Yeiser et al. 2020) as part of the modern quail management strategy (Stribling and Sisson 2009) have likely aided in further stabilizing or increasing populations on our area despite mild climatic changes. Future research should explore how intensive cultural practices may serve as climate mitigation strategies on the fringe of the bobwhite range.

MANAGEMENT IMPLICATIONS

The present rate of change regarding the timing of the onset, duration, or termination of breeding is very minimal and should not currently warrant any changes in management on intensively managed bobwhite properties. Research in the future should continue to monitor how bobwhite are responding to climate change to ensure that management is optimized to benefit population growth and expansion. If there is future evidence that the bobwhite breeding season is beginning sooner by a matter of weeks, is of shorter duration, or is being impacted by weather extremes, it could abbreviate an already short window of time where it is logistically and biologically feasible to manage bobwhite habitat. Significant changes in the future to nesting chronology patterns could warrant changes to the timing of the hunting season, prescribed burning, and other pre-breeding-season activities (i.e., timber harvesting, mowing, and dog training); however, our results suggest changes are not necessary at this time.

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