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Long-term, climate-driven phenological shift in a tropical large carnivore

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Understanding the degree to which animals are shifting their phenology to track optimal conditions as the climate changes is essential to predicting ecological responses to global change. Species at low latitudes or high trophic levels are theoretically expected to exhibit weaker phenological responses than other species, but limited research on tropical systems or on top predators impedes insight into the contexts in which these predictions are upheld. Moreover, a lack of phenological studies on top predators limits understanding of how climate change impacts propagate through entire ecosystems. Using a 30-y dataset on endangered African wild dogs (*Lycaon pictus*), we examined changes in reproductive phenology and temperatures during birthing and denning over time, as well as potential fitness consequences of these changes. We hypothesized that their phenology would shift to track a stable thermal range over time. Data from 60 packs and 141 unique pack-years revealed that wild dogs have delayed parturition by 7 days per decade on average in response to long-term warming. This shift has led to temperatures on birthing dates remaining relatively stable but, contrary to expectation, has led to increased temperatures during denning periods. Increased denning temperatures were associated with reduced reproductive success, suggesting that a continued phenological shift in the species may become maladaptive. Such results indicate that climate-driven shifts could be more widespread in upper trophic levels than previously appreciated, and they extend theoretical understanding of the species traits and environmental contexts in which large phenological shifts can be expected to occur as the climate changes.

phenological shift | climate change | African large carnivore | predator ecology | reproductive success

Significance

As a result of climate change, many species are shifting their timing of important life history events. However, the lack of investigation into apex predators limits understanding of upper trophic–level responses to long-term change and the ecological consequences of any such responses. Using a 30-y dataset on African wild dogs, we document a major climate-induced phenological shift in a large mammalian carnivore. Contrary to expectation, this shift may be contributing to lower reproductive success, highlighting the complexity of species' abilities to cope with climate change. Results suggest that climate-driven shifts could be more widespread among top predators than previously appreciated, and they demonstrate how climate change can affect top-down influences on ecosystems by changing the ecology of uppermost trophic levels.

Shifts in the timing of life history events, or phenological shifts, are one of the most well-documented ecological responses to global climate change (1, 2). In temporally varying environments, many species have evolved to synchronize the timing of seasonal reproduction to match optimal biotic (e.g., food resources) or abiotic (e.g., ambient temperature) conditions (3, 4). As climate change alters the timing of these ephemeral periods, species may adjust the timing of their reproduction to track these changes (5, 6) or else risk a phenological mismatch with optimal conditions (7, 8). Given the important ecological and evolutionary consequences of mismatched reproductive phenology (9), there is a critical need to assess species' phenological responses and associated outcomes to ongoing climate change (2).

Despite widespread interest in this subject (2, 6, 10), major gaps in phenological research hinder the ability to predict species' responses to climate change across diverse geographies, taxa, and trophic levels (2). The vast majority of phenological studies occur at high latitudes in the northern hemisphere, limiting understanding of latitudinal relationships between climate change and the direction, rate, and magnitude of phenological shifts (6) (Fig. 1*A*). For example, species are hypothesized to shift phenologies faster at higher latitudes (10), but lack of representation in the tropics precludes rigorous testing of this expectation (6). Furthermore, while most studies show an overall trend toward phenological advancement (e.g., earlier breeding) in response to long-term climate change (2, 6, 10), there is limited understanding of the geographical or biological context in which phenological delays (i.e., a positive correlation between phenological date and year) occur (11, 12).

Taxonomic disparities further hamper insights into the prevalence and context of phenological shifts. In particular, little research to date has examined the existence of phenological shifts in top trophic levels such as large mammalian carnivores (6, 13). Apex predators may show limited phenological responses to climate change given time lags or opposing impacts as climate change effects move up the food chain (13, 14). For example, secondary consumers generally show less phenological sensitivity to climate changes than lower trophic levels that have more direct links to bottom-up environmental processes (2, 6, 15, 16). Understanding the degree to which upper trophic levels are shifting phenologies in response to long-term warming is imperative given the

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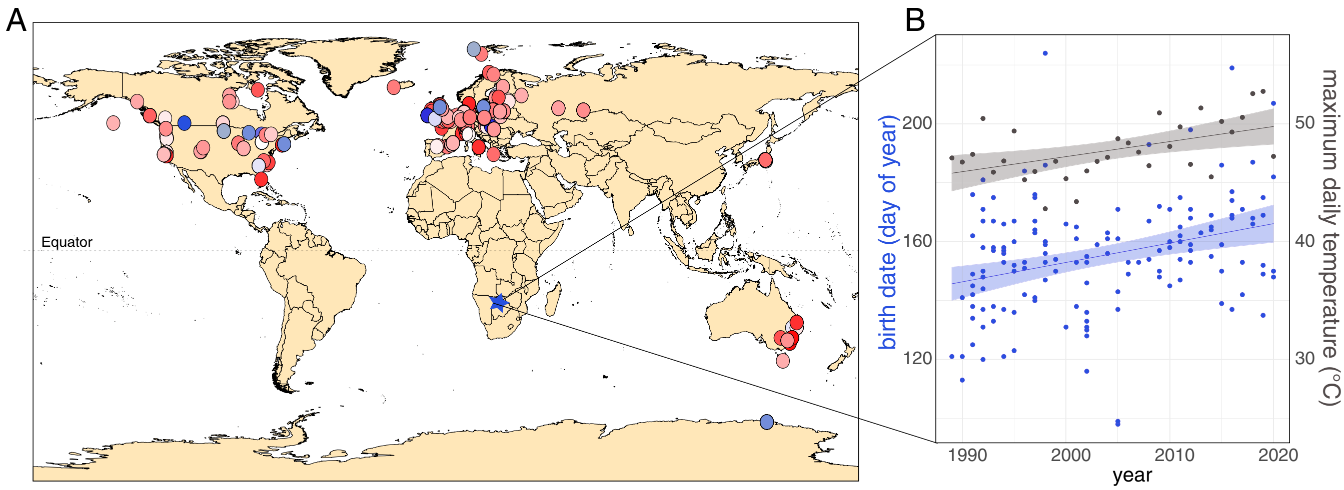

Fig. 1. (*A*) Map of published phenological studies of animals analyzed in Cohen et al. (6) (circles), highlighting limited geographic coverage in tropical systems. Red points indicate advancements in phenology over time; blue points indicate delays. Our study site, denoted by the blue star, has been added. Adapted with permission from ref. 6. (*B*) African wild dog birthing dates (blue) and maximum daily temperatures (gray) by year from 1989 to 2020 at our study site. Each birth data point represents a separate pack-year (n = 141). Lines represent linear regression estimates (mixed-effects regression for birthing dates); shading represents the 95% CIs.

keystone role that many top predators like large mammalian carnivores have in maintaining healthy ecosystems. Yet large carnivores remain among the most understudied taxa in this research domain (13). Long-term studies on large carnivore phenology are challenging because large carnivores are wide ranging and are often cryptic or nocturnal, making them difficult to monitor over long timescales (17). Thus, while there has been evidence of phenological shifts in small carnivorous mammals (primarily rodents) (18–20), a long-term phenological shift has not yet been documented in any large mammalian carnivores.

Here, we address this gap by using a unique 30-y time series to investigate the effects of climate change on the reproductive phenology and success of an endangered tropical large carnivore, the African wild dog (*Lycaon pictus*). African wild dogs are sensitive to maximum daily temperature, which has been shown to strongly influence behavior (21), reproductive success (22), and timing of reproduction in the species (3). Indeed, a large comparative study across Africa demonstrated that in latitudes with predictable seasonality, average maximum daily temperature, rather than precipitation or primary production, is the primary driver of wild dogs' seasonal reproduction timing (3). In those regions, wild dogs synchronize breeding with the coolest times of the year (3). This is hypothesized to provide a selective advantage by aligning the dogs' approximately 90-d denning period following birth—the most energetically demanding time of the year—with optimal weather conditions for hunting (22). African wild dogs are therefore a model species to investigate potential effects of climate warming on phenology in a large mammalian carnivore. Moreover, potential climate change effects on the species' breeding behavior are of substantial conservation concern, as African wild dogs are an endangered species with declining population trends across most of its range (23), and temperatures across their range are projected to continue rising (24).

Our study takes advantage of long-term monitoring of African wild dogs from 1989 to 2020 in northern Botswana (centered at 23° 38′ E, 19° 30′ S). This study population forms part of the world's largest African wild dog population, which extends from northern Botswana into western Zimbabwe, eastern Namibia, southwestern Zambia, and southeastern Angola (23). In this region, climate warming has driven increased temperatures over the last several decades, including record highs in recent years (25). We used ground-based monitoring data on birthing dates, demography, and pack characteristics from 60 packs and 141 unique pack-years to test the hypothesis that wild dogs have shifted their reproductive phenology in synchrony with long-term, climate-driven local warming. Specifically, we used 1) linear regression to evaluate long-term trends in birthing dates and resultant longitudinal changes in temperature during birthing and denning, 2) generalized additive models to evaluate potential underlying environmental drivers of any observed phenological shift; and 3) generalized additive models to evaluate the effect of temperature during multiple stages of the reproductive cycle on reproductive success.

Results

Monitoring data revealed that African wild dog birthing dates have shifted 22 days later on average over 30 years (linear mixed-effects regression $\beta = 0.75$, SE = 0.26, $P = 0.004$, 95% CI = 0.25 to 1.26), from an average of May 20 in 1990 to 1991 to June 12 in 2019 to 2020 (Fig. 1*B*). Generalized additive mixed models (GAMMs) revealed that this shift was strongly driven by changes in ambient temperature in the study area (see Fig. 3*A* and *SI Appendix*, Table S1), which saw an approximately 1.6 °C rise in average maximum daily temperature and an approximately 3.8 °C rise in annual maximum temperature from 1989 to 2020 (Fig. 1*B*). This long-term rise in maximum daily temperature accords with corresponding rises in maximum dawn and dusk temperatures (*SI Appendix*, Fig. S1), when African wild dogs are most physically active (22). Maximum daily temperature andaverage rainfall in the preceding year were retained in a top-ranked GAMM predicting birthing phenology, with higher maximum temperatures nonlinearly predicting later birthing dates (see Fig. 3*A*). Furthermore, including maximum temperature in the model reduced the linear effect of year on birthing dates (GAMM parametric estimate for year $\beta =$ 0.54, SE = 0.27, $P = 0.05$, 95% CI = −0.04 to 1.00), indicating a strong effect of temperature on the birthing trend.

To evaluate how this shift may impact thermal exposure, we examined temperatures across the annual cycle and during birthing and denning across years. We found that the phenological

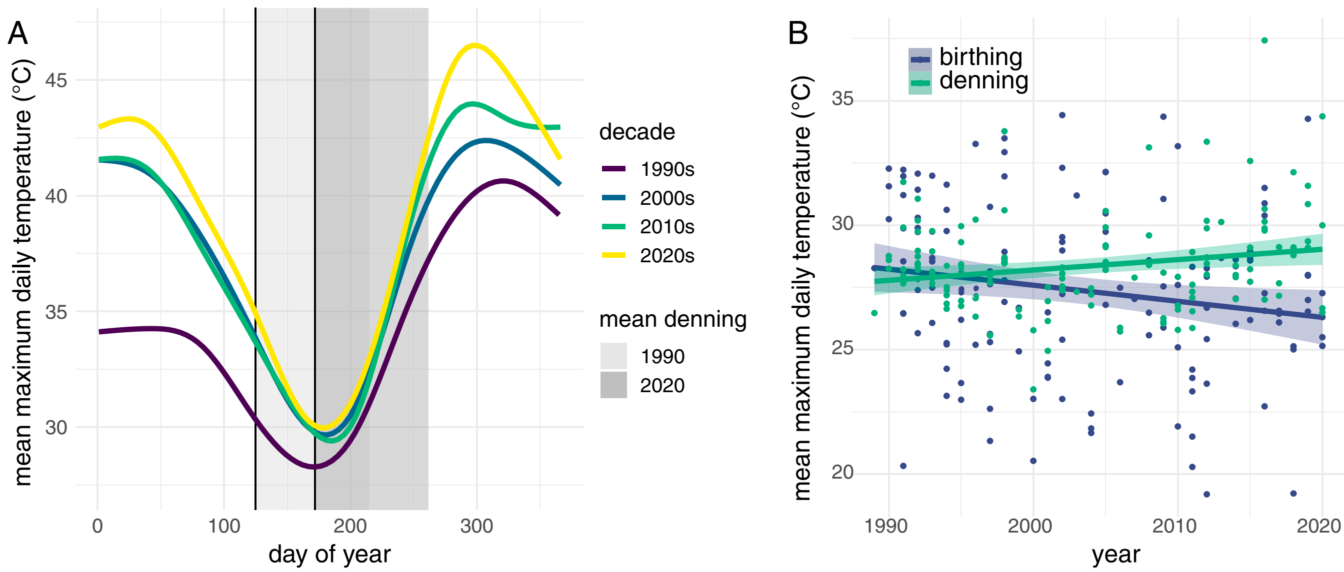

Fig. 2. (*A*) Average maximum daily temperatures in the study area over the annual cycle by decade. Vertical lines and shading represent the average birthing date and denning periods in 1990 (light gray) and in 2020 (dark gray), selected for demonstration. (*B*) Maximum daily temperatures during African wild dog birthing dates (purple) and 90-d denning periods (green) by year from 1989 to 2020. Each point represents a separate pack-year (n = 141). Lines represent linear mixed-effects regression estimates; shading represents the 95% CIs.

shift has pushed birthing dates toward the annual nadir of daily temperatures (Fig. 2*A*), with the number of days between births and the annual temperature nadir in each year declining over time (linear regression β = −0.82, SE = 0.37, P = 0.03, 95% CI = −1.55 to −0.09). Consequently, over 30 years, temperatures on birthing dates have remained relatively stable despite warming annual temperatures (linear mixed-effects regression β = −0.06, SE = 0.04, P = 0.16, 95% CI = −0.15 to 0.025). In contrast, whereas average denning periods in early years of the study overlapped with the coolest temperatures of the year, the phenological shift has pushed recent denning periods toward warmer temperatures in the annual cycle (Fig. 2*A*). Accordingly, average maximum daily temperatures during the 90-d denning period have significantly increased (linear mixed-effects regression β = 0.06, SE = 0.03, P = 0.04, 95% CI = 0.004 to 0.12) from a mean maximum temperature during denning of 28.5 °C in 1990 to 1991 to 30.0 °C in 2019 to 2020 (Fig. 2*B*).

To investigate potential downstream consequences of the phenological shift, we examined the effects of temperature on reproductive success, since African wild dog pup recruitment is related to ambient temperature in other study regions (22). We used model selection to select among a series of candidate GAMMs that regressed the pup litter size during the denning period with temperature and/or rainfall during conception, birthing, and/or denning, while controlling for the number of adults in the pack (i.e., pack size), which has been shown to positively correlate with reproductive success (22, 26). The two top models (difference in corrected Akaike Information Criterion [ΔAICc] ≤ 2) predicting denning litter size included only denning temperatures (maximum and mean, respectively; Pearson's

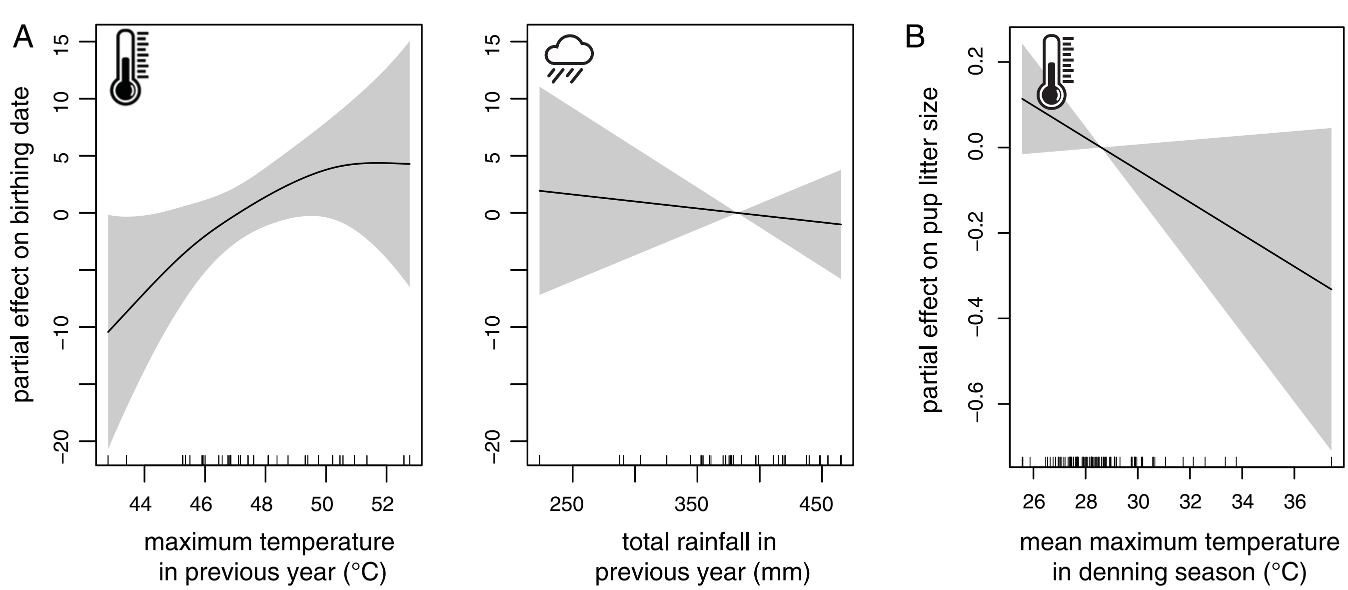

Fig. 3. Partial response curves (smooth terms) from a top-ranked GAMM showing (*A*) the influence on the previous year's environmental conditions on birthing dates the following breeding season, and (*B*) the influence of maximum daily temperatures during the denning season on the number of pups sighted after den emergence (estimated age 1 to 3 mo). Predicted GAMM values are the solid black line; shading represents twice the SE. Rugplots at the *Bottom* of each panel show data distributions.

Table 1. Summary statistics of top-ranked Poisson GAMM predicting pup litter size during denning

Predictor	Estimate	SE	95% CI
Mean maximum daily temperature during denning*	−0.0657	0.0374	−0.1458, 0.0006
Pack size	0.0252	0.0061	0.0131, 0.0371
Year	−0.0049	0.0036	−0.0120, 0.0022

*Modeled as a smooth (nonparametric) term but showed a linear relationship with litter size.

$\rho = 0.96$) as environmental predictors (*SI Appendix*, Table S2). Higher maximum daily temperatures during denning periods decreased reproductive success (Fig. 3*B* and Table 1). The third-ranking model (ΔAICc = 2.67) included a weak negative effect of rainfall during the denning season on denning litter size (*SI Appendix*, Fig. S2). We also explored the effect of environmental conditions on the number of pups surviving to 1 year of age given the denning litter size, but environmental conditions were not retained in top-ranked models (*SI Appendix*, Table S3).

Discussion

Across animal taxa, many species time key life history events such as reproduction with the timing of optimal biotic or abiotic conditions. Understanding the degree to which animals are shifting their phenology to track these conditions as the climate changes is essential to predicting ecological responses to global change. Examination of these effects across a diverse range of taxonomies and geographies is needed to substantiate generalizable patterns, such as a negative correlation between trophic level and climate sensitivity (15), and the contexts in which those generalities fail. Here we document a phenological delay in reproduction in a top predator species, African wild dogs, of approximately 1 week per decade as a result of long-term warming. This represents a shift of over twice the average absolute rate observed across the animal kingdom (6). Thus, the expectation that top trophic levels should exhibit less phenological sensitivity to climate should be carefully qualified (2). To our knowledge, this study represents the first to record a phenological shift in a large mammalian carnivore in tandem with climate change and extends theoretical understanding of the species traits and environmental contexts in which large phenological shifts occur.

The phenological shift observed here provides insight into the ultimate and proximate processes driving phenological responses to climate variability and change. The negative relationship we found between denning temperatures and reproductive success likely reflects an ultimate pressure to rear pups in cool weather (3). This finding supports those from other African wild dog populations demonstrating a negative relationship between pup survival or juvenile recruitment and denning temperatures (22). This could potentially be a function of temperature constraints on lactation in the breeding female. According to the heat dissipation limit hypothesis, the activity and reproductive output of endotherms is limited by their ability to dissipate heat (27); supporting this hypothesis, milk yield is suppressed in lactating mice and domestic cows during periods of heat stress (27, 28). However, it is not known whether or which temperature thresholds may exist that would reduce lactation in African wild dogs to the extent that it would limit reproductive success. Another plausible mechanism is the effects of temperature on wild dog hunting behavior. At a pack level, denning is the most energetically demanding time of year for this cooperatively breeding species, as food must be frequently provisioned to pups and the lactating female and commuting back to the den to do so confers additional costs (22). African wild dogs are cursorial predators; therefore, their hunting activity is thermally constrained due to the limiting effects of heat accumulation on running performance (29). As a result, wild dogs reduce both their amount of time hunting and overall activity levels on hot days (21, 22). Therefore, they may be under selective pressure to align denning with cool temperatures in order to maximize hunting profitability.

The proximate cues used for birthing appear to be disconnected, however, from ultimate drivers to den in cool weather. Our finding that temperatures on birthing dates have not significantly changed over three decades despite a significant long-term rise in ambient temperatures suggests that wild dogs are synchronizing parturition with a narrow thermal window, as proposed by previous comparative work (3). Our findings further support previous research that found a strong relationship between African wild dog birth timing and temperature, but little effect of rainfall (3). Thus, rainfall or primary production are unlikely to be important cues for reproduction in the species relative to temperature. Photoperiod (i.e., day length) has also previously been suggested as a possible proximate cue for reproductive activity in wild dogs (3) as well as gray wolves (*Canis lupus*) (13), although this remains untested. Photoperiod is a trigger for the seasonal reproduction of many mammals globally (30, 31), and supporting this hypothesis, wild dogs translocated to zoos in the northern hemisphere breed approximately 6 mo later than populations at equivalent latitudes in the southern hemisphere (3). However, the long-term phenological shift in breeding observed here is not consistent with a cue based on photoperiod alone. Like photoperiod, ambient temperature thresholds can also trigger the onset of breeding in many taxa (32), including mammals (33, 34). We found support for preceding temperature conditions as drivers of wild dog parturition timing. In addition, our result that wild dogs are delaying parturition on pace with ambient warming is consistent with a hypothesis that ambient temperature, or an interaction between temperature and photoperiod, may be an external environmental cue guiding the timing of reproduction in the species.

The decoupling of environmental cues triggering a life history event from those affecting reproductive success is concerning given ongoing climate change. In some species, the climate signals animals rely upon to time parturition may be decoupled from those needed to optimally time periods of intensive parental investment following birth (13). In theory, phenological shifts in response to climate change may therefore create a match with optimal conditions for one stage of the reproductive cycle but a mismatch for another critical stage (13). Our findings provide an empirical example of this phenomenon, in which a phenological shift associated with tracking cool temperatures for parturition has resulted in even warmer temperatures experienced during the denning period, which are linked to lower reproductive success. This phenomenon is analogous to an evolutionary trap, in which rapidly changing environments decouple the cue an organism uses to guide its behavior from that cue's fitness outcome (35, 36). Thus, African wild dogs may be experiencing a "phenological trap," where the cues used for shifting the timing of parturition may ultimately lower fitness and become maladaptive. In addition, the overall duration of cool winter temperatures in our study area appears to be contracting in recent decades (Fig. 2*A*), which may further constrain optimal reproduction timing. These results shed light on the complexity species face in their ability to cope with climate change.

Despite long-term warming and the negative relationship between temperature and reproductive success, we detected only weak support for a negative effect of year on denning pup count (Table 1 and *SI Appendix*, Fig. S3). This is plausibly because interannual variability in both temperature and reproductive success is very large relative to the overall trend in warming. In particular, the annual increase in denning temperatures was very small ($\beta = 0.05$, SE = 0.02) compared to the residual variance ($\sigma^2 = 2.89$), which is apparent in Fig. 2*B*. Thus, high between-year variation in temperature may mask across-year effects of a gradual warming trend. In addition, pack sizes have slightly increased over time, which may counterbalance the effects of rising temperatures (*SI Appendix*, Fig. S3). Moreover, little is known about long-term trends in other factors that influence pup survival during the denning season in this system, such as competitor or prey densities (37) or high-quality denning habitat availability (38). It is possible that changes in any of these factors may buffer against the effects of long-term warming, although data are lacking to rigorously test this. These findings affirm that long-term monitoring is often a necessary tool for elucidating the causes of changes in reproductive success, particularly for differentiating gradual changes from year-to-year variability.

Climate-induced shifts in large carnivore breeding phenology likely have important impacts on trophic interactions and community dynamics. The combination of a phenological delay pushing denning into warmer weather, combined with long-term rises in ambient temperature, has broad implications for predator–prey interactions and intraguild dynamics. Temperature is already known to affect large carnivore activity levels (22), diurnal activity patterns (21), and hunting success (39), but the long-term phenological shift we document here also threatens to alter critical spatiotemporal partitioning strategies of African wild dogs, potentially elevating already limiting suppression by their main predator. Lion (*Panthera leo*) predation is a key source of African wild dog pup mortality, which is highest during the denning and immediate postdenning periods (40). Consequently, African wild dogs attempt to reduce the risk of ambush by lions by selecting den sites with good visibility and in habitats with low lion densities during the denning season (38, 41). During dry seasons (May to September in our study area), lions aggregate near permanent water sources where prey are concentrated (42, 43), whereas lions and their prey range more widely and unpredictably following the rains. As wild dog denning is pushed toward the wet season (typically November to March), rain-driven vegetation growth may decrease visibility, and less predictable ranging by lions may increase the risk of lion encounters and predation during the pups' most vulnerable stage. Similarly, it is unknown whether other species in the system, including important prey, have similar phenological responses to long-term warming. Whether predators and their prey shift phenology at similar rates has important ecological consequences (7). While currently speculative, such dynamics require further investigation to document how climate change impacts cascade through complex multipredator, multiprey systems.

Climate change is often conceptualized as imposing bottom-up changes in the ecosystem (44, 45), but our study highlights how climate change can exert top-down influence by changing the behavior or ecology of uppermost trophic levels. In marine systems, top predators are widely regarded as effective sentinels of climate impacts in their ecosystem because they integrate information across multiple trophic levels and spatiotemporal scales (46–50). Our study indicates that African wild dogs and other climate-sensitive terrestrial predators may also be effective climate sentinels— i.e., species that respond to climate variability or change at relevant timescales in a measurable and interpretable way and can indicate broader climate-driven changes in the ecosystem (46). Our study helps fill an important taxonomic and geographic gap in the body of global change biology literature, and our findings suggest that long-term, climate-driven phenological shifts could be more widespread in upper trophic levels than previously recognized. Finally, this work emphasizes how ongoing monitoring to extend long-term time series, such as that presented here, is critical for detecting behavioral and demographic shifts as the climate continues to change.

Methods

Study System. Our study site (circa 2,700 km^2, centered at 23° 38′ E, 19° 30′ S) lies on the eastern side of the Okavango delta in northern Botswana, and includes parts of the Moremi Game Reserve as well as adjoining wildlife management areas. This region is characterized by highly seasonal variation in temperature, with cool, dry winters typically extending from May to September, and warm, rainy summers in November to March (Fig. 2*A*). Here, and in other latitudes with predictable seasonal variation, African wild dogs exhibit seasonal reproduction followed by an approximately 90-d denning period during winter (3). Long-term monitoring of the African wild dog population was initiated in our study area in 1989, and has run continuously to the present day. Our dataset included 60 unique packs monitored for an average of 2.38 years each (range, 1 to 7 y; *SI Appendix*, Fig. S4). From these monitoring data, we extracted birthing date (range, April 8 to August 12; mean June 4), adult pack size (i.e., number of individuals >12 mo of age: range, 2 to 30; mean 10), litter size at first sighting of den emergence (occurs between 1 and 3 mo of age; range, 3 to 16; mean 10), and number of pups surviving to 1 y (range, 0 to 11; mean 4) for all pack-years for which data were recorded between 1989 and 2020. In rare cases, a subordinate female in a pack birthed a litter, which were consistently later than those birthed by dominant females (3). As such, we removed data points where a subordinate female was the birthing mother, resulting in removal of 9 pack-years out of an original 150, with the remaining 141 pack-years retained for analysis.

Environmental Data. For our analyses we examined the effect of maximum daily temperature, as this is a significant and most commonly used predictor of African wild dog behavior and demography (3, 21, 22). We modeled historical hourly temperatures from 1989 to 2020, using microclimate modeling centered at the core of our study area (23° 38′ E, 19° 30′ S) and computed at a local height of 1 m available from the R package NicheMapR (51). Hourly temperatures were used to calculate the maximum daily temperatures used for analysis. We confirmed that maximum daily temperatures modeled in our study area correlated with observed maximum temperatures recorded at the Maun airport weather station (23° 25′ E, 19° 58′ S), which is approximately 40 km from the study area boundary (Pearson's $\rho = 0.75$, $P \ll 0.01$, 95% CI = 0.74 to 0.76). Although previous research comparing sites across Africa, including ours, found no clear association between birth timing in African wild dogs and rainfall (3), we also explored variation in monthly accumulated rainfall obtained from the closest weather station (Maun Airport) as a potential alternative driver of changes in reproduction phenology and reproductive success.

Data Analysis. To examine longitudinal trends in birthing dates, temperature on birthing dates, and temperature during denning periods, we used linear mixed-effects regression with year included as both a fixed effect (as a continuous variable to capture trends over time) and random effect (as a factor variable to capture unexplained heterogeneity between years) as well as pack identity as a random effect.

To examine potential environmental drivers of the phenological shift, we fitted GAMMs with a Gaussian distribution to relate variation in birth timing to variation in environmental covariates. Environmental covariates were included as smooth terms to consider nonlinear relationships with phenology; these included temperature and rainfall in May (average month of parturition), March (average month of conception) of each year, September of the preceding year (average end of denning period), and averaged over the current year and preceding year. Year was included as a continuous linear term to account for changes over time. Pack and year (as a factor) were included as random effects.

To examine the effect of temperature on reproductive success, we fitted GAMMs with a Poisson distribution. The response variable was the count of pups first sighted after emergence from the den (estimated age 1 to 3 mo) as a synoptic measure of reproductive success, since litter size at birth is unknowable as newborn pups do not leave the den (22). We checked for overdispersion in the data using the performance R package (52); no overdispersion was detected (dispersion ratio for top-ranked model $= 0.632$, $P = 0.997$). Smooth terms to examine nonlinear relationships with environmental covariates included mean and maximum daily temperature and monthly rainfall during the denning period, on the birthing day, and during the conception period (calculated as the 2-wk period centered on 72 days before birth; refs. 3 and 53). Year (continuous) and pack size were included as linear terms. Pack size was included as an explanatory variable because it is associated with increased hunting success and adult and pup survival in wild dogs (22, 26). Dominance status of the breeding female is also likely to affect reproductive success, but it was not included as a covariate since subordinate females were excluded from analysis. For yearling survival, we examined the effects of temperature and rainfall covariates during the 6 months postdenning, while additionally controlling for pup litter size during denning and pack size. For both initial pup count and yearling survival analyses, pack and year (as a factor) were included as random effects.

For each of the above GAMM analyses exploring environmental drivers of the phenological shift and of reproductive success, we used AIC model selection corrected for small sample size to select among a series of candidate environmental covariates (54). Models with ΔAICc scores of 2 or less were considered as having equal support (55). For all models, we first checked for collinearity among predictors; predictors with a pairwise Pearson correlation $|\rho|$ greater than 0.7 were not included in the same model formula (56). Mixed-effects linear regression analyses were performed using the lme4 package (57); GAMMs were performed using the gamm4 package (58). All analyses were conducted in R version 4.1.0 (59).

Data Availability. All data reported in the manuscript and code used to generate analyses are available in GitHub (https://github.com/briana-abrahms/Wild-Dog-Phenology) (60) and Zenodo (https://doi.org/10.5281/zenodo.6581485) (61).

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