

Phenotypic plasticity in the timing of reproduction in Andean bears

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Abstract

Many factors influence whether mammals reproduce seasonally or continuously but disentangling them can be challenging in free-living species that are hard to observe. We described the seasonality of reproduction in Andean bears (*Tremarctos ornatus*) in NW Peru (6°26'S, 79°33'W) to test for phenotypic plasticity in response to extrinsic cues. To do so, we compared the mating behavior and birthdates of free-living bears to the birthdates of captive bears housed over a broad range of latitudes. Free-living bears were observed on 302 occasions over 6 years (967 field-days), and mating behaviors recorded 61 times from late Dec to Jan. The mean birthdate of 12 wild-born litters was 17 August (range = 23 Jun – 15 Oct), 57 ± 10 (SD) days after the winter solstice. Birthdates for 367 captive litters varied widely by comparison (range = 1 Jan – 31 Dec; mean = 14 ± 49 days after the winter solstice). However, captive bears in the tropics had fewer births in autumn and winter (71.4% of births) than captive bears at higher latitudes (96.8% of births; $P < 0.001$). Differences in seasonal reproduction among captive bears at high and low latitudes and captive and a free-living at tropical latitudes suggest that Andean bears display phenotypic plasticity in reproductive timing but influenced by photoperiod at high latitudes. Because photoperiodic effects were less evident at tropic latitudes, we suggest that seasonality in the timing of reproduction in the free-living bears we observed was influenced by seasonal variation in food abundance. The observed effect of photoperiod on reproduction in captive Andean bears at high latitudes may also imply that free-living bears at the southern edge of the range may be constrained in their ability to adjust reproductive timing to resource availability as environments change.

Introduction

The energetic costs of mammalian reproduction can be high but also vary over the reproductive cycle and across environments. Seasonal reproduction is therefore expected where individual fitness is maximized by incurring the most energetically costly events during seasonal peaks in food abundance (Baker, 1938; Arcese & Smith, 1988; Bronson, 1989). Seasonal reproduction is well-known in birds and mammals and often linked to variation in diet, food abundance, climate or predation pressure, particularly at high latitudes where photoperiod can also act as a reliable extrinsic cue (Findlay & Cooke, 1982; Bronson, 1989; Sinclair, Mduma & Arcese, 2000; Ogutu *et al.*, 2015). However, spatial and seasonal variation in primary production can also drive the evolution of seasonal reproduction at low latitudes, where variation in photoperiod is less pronounced (Bronson, 2009; Ogutu *et al.*, 2015). Elucidating such effects in free-living species is

challenging (Beehner *et al.*, 2006; Visser *et al.*, 2010; Huang *et al.*, 2012; Watts & Hahn, 2012; García-Díaz & Lizana, 2013) and the factors affecting seasonal reproduction in tropical species remain under-studied, particularly in some rare species of concern to conservation. Our goals here were to: (1) characterize reproductive seasonality in a tropical mammal, the Andean bear (*Tremarctos ornatus*); (2) identify potential cues affecting reproductive seasonality in captive and free-living Andean bears; and (3) speculate on the ability of Andean bears to respond to climate-induced environmental change.

Seven of eight extant bear species, including Andean bears, exhibit reproductive seasonality despite wide latitudinal variation in distribution (Spady, Lindburg & Durrant, 2007). Although Andean bears are thought to have originated in the north temperate zone (McLellan & Reiner, 1994; Soibelzon, Tonni & Bond, 2005), the species now inhabits a latitudinal range from c. 11°N to 23°S, with about two-thirds of

individuals occurring between 11°N and 11°S (Goldstein *et al.*, 2008; Cosse *et al.*, 2014). Bears in this more restricted range experience < 81 minutes of annual variation in photoperiod, compared to up to 170 minutes at the southern edge of the range. However, the effects of photoperiod and resource availability on the timing of reproduction in free-living Andean bears remain largely unknown given that anecdotal reports suggest they breed throughout the year (Peyton, 1980, 1999) but only two birthdates have been reported (January and June, both within 1° of the Equator; Castellanos, 2010, 2015).

Using data from captive bears, Spady *et al.* (2007) found that Andean bears were facultative, seasonal breeders at north temperate latitudes, similar to brown bears (*Ursus arctos*), American black bears (*U. americanus*) and Asiatic black bears (*U. thibetanus*), but displayed a 6-month shift in reproductive timing when housed south of the Tropics, suggesting a strong effect of photoperiod. Gerstner *et al.* (2016) also inferred an effect of photoperiod on seasonal change in body mass and food intake in captive Andean bears, in support of an hypothesis that photoperiod serves as a zeitgeber affecting reproductive timing in Andean bears at high latitudes (cf Follett & Follett, 1981; Nicholls *et al.*, 1988).

In contrast, theory and empirical studies of species that breed in the Tropics indicate that local environmental cues can become more influential than photoperiod as drivers of seasonal reproduction by entraining endocrine processes to food availability, climate or social conditions (Baker, 1938; Bronson, 1989; Sinclair *et al.*, 2000; Beehner *et al.*, 2006; Watts & Hahn, 2012). Applied to Andean bears, we might therefore expect to observe more variation in the timing of reproductive in populations subject to different environmental conditions but occupying similar tropical latitudes (Palmer *et al.*, 1988; Sinclair *et al.*, 2000; Spady *et al.*, 2007; Ogutu *et al.*, 2010).

Although seasonal variation in rainfall and food abundance are thought to be limited in the cloud forest habitats mainly occupied by Andean bears (Peyton, 1999), little is known about the resources potentially limiting their reproduction. However, because Andean bears also inhabit seasonally dry, tropical forest (Peyton, 1980), where photoperiodic cues are weak but environmental cues linked to variation in resource abundance are strong, we compared seasonality in the reproduction of captive and free-living occurring at similar latitudes to test facultative adjustment to environmental cues in addition to photoperiod.

Specifically, we studied a population of free-living Andean bears at -6 degrees latitude in dry tropical forest habitats of the coastal Andean foothills of northern Peru, an area with little variation in photoperiod but strong seasonality in moisture and temperature regimes capable of driving seasonality in food abundance (Brack Egg, 1986; Linares-Palomino & Ponce-Alvarez, 2009). Given these conditions and studies reviewed above, we expected to observe seasonality in the timing of reproduction and births of Andean bears that coincided with periods of food abundance. To test these ideas, we collected field observations and camera trapping data to document the mating behavior and birthdates of free-living Andean bears in relation to season. We also compared reproductive timing in free-living Andean bears to that of captive bears housed over 90° of latitude to test for evidence of phenotypic plasticity in

the response of Andean bears to cues known to influence reproductive timing in tropical and temperate mammals.

Materials and methods

Study area

We worked in the mountainous Peruvian watershed of the Rio La Leche (Pitipo, Lambayeque, centered at Cerro Venado at 6°26'S, 79°33'W); a biodiverse region of global conservation significance (Olson & Dinerstein, 2002) in which equatorial dry forest is the predominant plant community, with isolated remnants of lowland *Prosopis* forest (Linares-Palomino *et al.*, 2010). Bears occurred from *c.* 140–1300 m elevation in our *c.* 250 km² study area, where the mean annual temperature is 24°C (range 18°C–38°C) and annual variation in rainfall is high (mean = 108 mm, range *c.* 50 mm–1000 mm; Brack Egg, 1986; Linares-Palomino & Ponce-Alvarez, 2009), but concentrated in the months of March and April. A small number of streambeds held springs that provided water year-round, and sparse vegetation and steep terrain allowed bears to be observed directly as they traversed slopes or ridges *en route* to or from waterholes or feeding sites, including low elevation sites where the fruit of sapote (*Colicodendron scabridum*) is seasonally available. The loud, cracking sound of bears feeding on pasallo (*Eriotheca ruizii*) also aided our visual detection of bears. Observations reported here were collected from 22 March 2007 to 30 June 2013, during 967 field-days by one or more observers, distributed across years (*i.e.*, 92, 170, 139, 245, 167, 121 and 64 field-days from 2007 to 2013 respectively).

Reproductive seasonality in wild Andean bears

Detecting females and cubs using remote cameras and direct observations

From March 2007 to December 2013, bears were identified by recording their highly variable facial and chest markings while observing them directly, or indirectly using photographs taken opportunistically by human observers or at camera traps (Roth, 1964; Eck, 1969; Van Horn *et al.*, 2014). Camera traps were situated adjacent to nine high elevation springs distributed across the study area and used regularly by bears. Each trap comprised of one to two cameras fitted with passive infrared sensors (*i.e.* Cuddeback Excite, Reconyx RM 45 or MC65), placed *c.* 50 cm above ground to photograph the bears' face and chest (10 photographs per trigger, 24 hours/day), and checked every 10–30 days from 11 June 2008 to 30 June 2013 to change batteries and ensure proper operation.

Photographs of females and cubs were used to estimate birthdates based on the relative size of a cub to its mother (Van Horn *et al.*, 2015). The reliability of this method was assessed by asking three field workers to identify bears regularly encountered at camera traps in different photographs. Observers assigned 96% of 100 trials correctly, implying a kappa of 0.9, indicating 'almost perfect agreement' (Viera & Garrett, 2005).

Estimating date of birth of cubs located in natal dens

We located seven active natal den sites via intensive field survey and GPS telemetry. Den entry was inferred from the sudden absence of GPS collar transmissions, which led us to search around the last transmitted location. Once dens were located, photographs of cubs were taken using a 400mm telephoto lens at close range (c. 5–10 m) and their ages estimated as the midpoint of developmental stages described among captive bears: eyes beginning to open at 38–42 days; eyes fully open at 37–47 days, just walking at 57–75 days, cub first leaves den at 60–90 days (Bloxam, 1977; Aquilina, 1981; Molloy, 1989).

Unless noted, all quantities are expressed as $\bar{x} \pm \text{SE}$, and statistical significance refers to two-tailed $p = 0.05$. Statistical analyses were conducted in JMP 9.0.3 (SAS Institute Inc., Cary, NC).

Estimating date of birth of cubs first detected outside natal dens

Over 6 years, we compiled photographs of females and cubs at the natal den and/or when first detected away from their natal dens at waterholes to estimate birthdate. The birthdates of cubs < 180 days old were estimated by averaging ages assigned by three human observers asked to compare (1) the relative size of a cub to its mother (measured as shoulder height) and (2) three postcranial traits described in Van Horn *et al.* (2015), while noting the position of the mother and cub relative to the camera using visual landmarks. We were unable to estimate a birthdate for one litter of twins and excluded them from analysis. We estimated implantation date based on a gestation period of 60 days (Dehnhard *et al.*, 2006) to emphasize that implantation determines birthdate and may be more closely linked to a zeitgeber than reproductive behavior (Spady *et al.*, 2007).

Observations of behaviors linked to mating

From 22 March 2007 to 30 June 2013, we documented all mating events by free-living bears observed during 908 days of fieldwork conducted throughout the year. All data were collected by the same two to three skilled observers, who scanned valleys, waterholes and cliffs from adjacent ridges until a bear was sighted. Subsequent observations were made from distances of 20–500 m to record the identities of all adult bears within 50 m of each other (e.g. 'pairs'), and the occurrence of mating, agonistic behavior (i.e. threats, displays and fights) and agonistic vocalizations (i.e. vocalizations indicative of agonistic encounters not directly observed). Because it was not possible to identify individual bears in all observations, we only recorded one instance of a given behavior observed for any pair of bears observed in the same location on a given day.

Evaluating reproductive seasonality using captive Andean bear data

We extended work by Spady *et al.* (2007) by collecting birthdates of captive Andean bears over a broad latitudinal range

using the international studbook through 31 December 2011 (Hall, 2012). More recent birthdates were collected directly from zoos in North and South America, including South American zoos not in Hall (2012). All litters with birthdates reported with precision of ≤ 5 days, and with known mothers were analyzed, for a total of 376 birthdates (356 from Hall, 2012; which included Spady *et al.*, 2007; 11 from other sources), over 60 years (17 February 1953–2 January 2013), 70 zoos and 90° of latitude. Twenty-five litters were born in the Southern Hemisphere and 342 litters were born in the Northern Hemisphere (Fig. 2).

We expected that reproduction in captive bears might respond similarly to external environmental cues, which also affect free-living, but did not expect temporal shifts in birthdate across latitude. Instead, we focused on seasonality in birthdate, as estimated by the spread of birthdates recorded in latitudinal bands likely to represent bears subject to similar external environmental cues. Specifically, we characterized birth seasons in relation to solstices and equinoxes and grouped birthplaces into four latitudinal zones for analysis: tropical ($\leq 23.5^\circ$ N or S), low temperate (23.5–35° N or S), mid temperate (35–55° N or S) and high temperate (55–67° N or S).

We elected to pool birthdates of captive bears, given that these data were collected over six decades, probably spanned a variety of husbandry practices that changed temporally, and are therefore best explored conservatively. Specifically, we compared the seasonal occurrence (i.e. spring, summer, autumn, winter) of captive births with a G-test, after pooling births into two zones (Tropics, all other data) to ensure expected cell frequencies ≥ 5 (Sokal and Rohlf 1981). Because environmental cues linked to photoperiod vary more at high than low latitudes, we also expected to observe less variation in birthdates at high than low latitudes. We tested this expectation by regressing the Standard Deviation (SD) of pooled birthdates on distance from the Equator measured as midpoint of Tropical, Low Temperate, Mid Temperate, High Temperate zones and in 5° latitude classes. Because pooling may result in the loss of information, we also explored linear fits to the data and examined the residuals of observed minus predicted birthdate, regressed on variation in day length, latitude and distance from the equator. Because all analyses gave similar results, we chose to report only the results of pooled analyses. Unless otherwise noted all quantities are expressed as $\bar{x} \pm \text{SE}$, and statistical significance refers to two-tailed $p = 0.05$. Statistical analyses were conducted in JMP 9.0.3 (SAS Institute Inc., Cary, NC).

Results

Timing of births and mating behavior in wild Andean bears

Seven wild-born litters (six singletons, one twin litter) observed in their natal dens had birthdates from 23 June to 16 August (mean = 27 July \pm 8; Fig. 1). Of seven additional litters first observed outside their den, five were

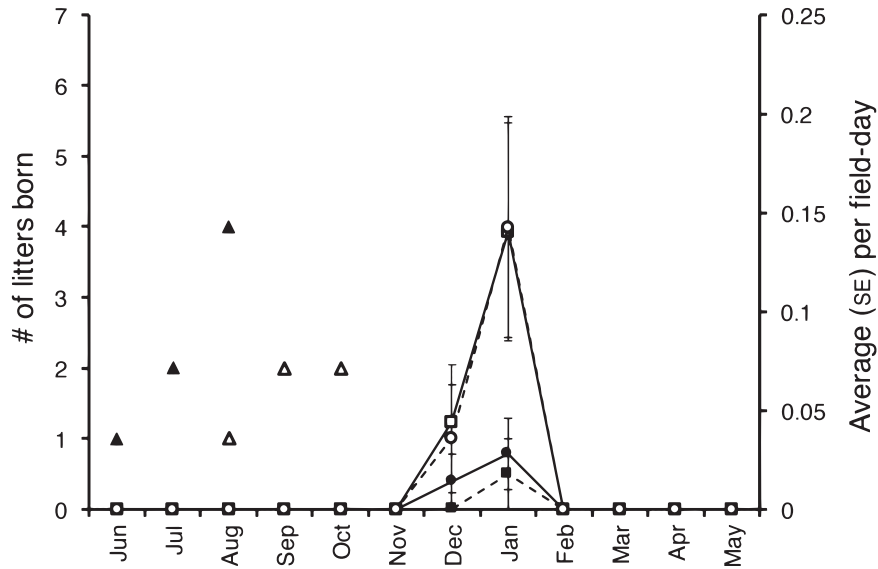


Figure 1 Data collected from wild Andean bears at Cerro Venado during 967 field-days from 22 March 2007 to 30 June 2013. Filled triangles indicate births of litters seen in their natal den. Open triangles indicate births of litters first seen after leaving their natal den. Filled squares indicate copulations. Open squares indicate pairs of adult bears. Filled circles indicate agonistic encounters between adult bears. Open squares indicate agonistic vocalizations by adult bears.

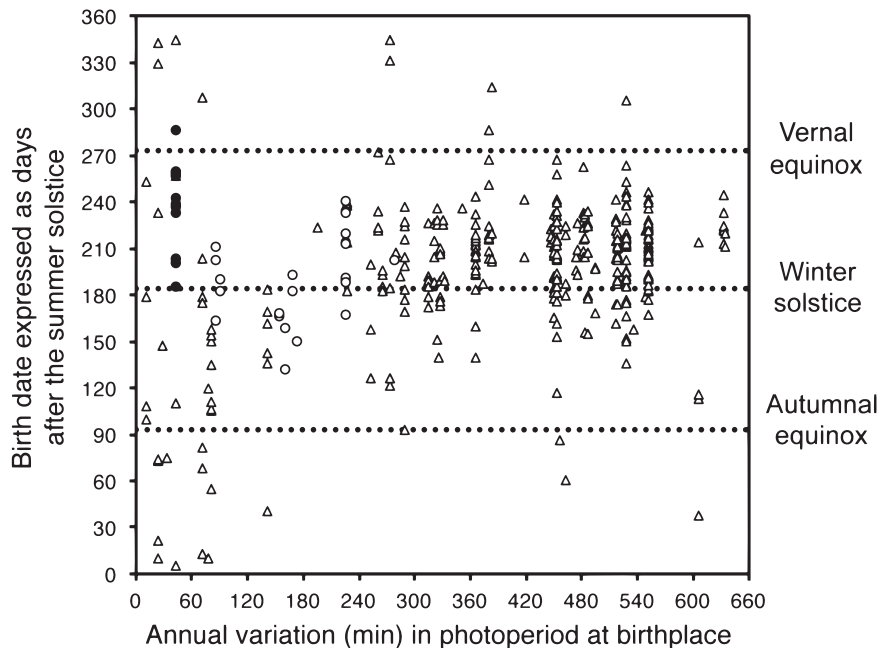


Figure 2 Birthdates of litters of Andean bears in relation to photoperiod and season at birthplace. Open triangles indicate births in captivity in the Northern Hemisphere ($n = 342$). Open circles indicate births in captivity in the Southern Hemisphere ($n = 25$). Filled circles indicate births in the wild from the Cerro Venado study area ($n = 12$).

assigned birthdates from 19 August to 15 October (Fig. 1, Fig. 2; mean = 15 September; ± 1 SD error = 22 August–8 October), but two were not assigned birthdates because they were estimated to be > 180 days old when first observed. By subtraction, the mean date of implantation for litters first observed at or away from their dens were 28 May (± 1 SD error = 6 May–19 June) and 17 July (± 1 SD error = 23

June–9 August) respectively. The mean birthdate of all 12 wild litters noted above was 17 August (23 June–15 October, ± 1 SD error = 14 July–19 September); 57 ± 33 days (range = 1–123 days) after the winter solstice, implying a mean date of implantation of 18 June ± 33 days (24 April–16 August), or -3 ± 10 days (range -59 – 57) relative to the winter solstice.

Of 302 opportunistic observations of Andean bears, all 61 instances of mating behavior were recorded in December or January (Fig. 1). These observations comprised 26 pairs of bears, three copulations (involving three males, two females), six agonistic encounters and 26 agonistic vocalizations (Fig. 1).

Timing of births among captive Andean bears

Most (92.9% of 367) birthdates of captive litters occurred in the autumn and winter across latitudinal zones (Table 1, Fig. 2). However, births were shifted toward autumn in the Tropics, and toward winter outside the Tropics; 51.8% of 56 births occurred in autumn versus 19.6% in winter in the Tropics, compared to 15.8% of 311 births in autumn versus 81% in winter outside the Tropics ($\chi^2 = 46.3$, $p < 0.001$). In addition, dispersion in the birthdates of captive bears increased closer to the Equator, with significantly more births occurring outside of autumn or winter in the Tropics (28.6% of births) versus 3.2% occurring outside of autumn or winter outside the Tropics ($G = 87.78$, $DF = 3$, $p < 0.001$). Similarly, with birthdates pooled into 5° latitude classes, or into broad latitude zones (i.e. Tropical, Low Temperate, Mid Temperate, High Temperate), we observed an inverse relationship between variation in birthdate (measured as SD) and distance from the Equator ($n_{\text{classes}} = 12$, $DF = 10$, $R^2 = 0.46$, $p = 0.015$; $n_{\text{classes}} = 4$, $DF = 2$, $R^2 = 0.93$, $p = 0.038$ respectively).

Discussion

Seasonality of reproduction in wild Andean bears

We provide the first evidence of seasonality in reproduction in wild Andean bears. The birth of a free-living Andean bear was reported by Castellanos (2010) to have occurred in January in cloud forest at about 1°N. Castellanos (2015) reported a second wild birth in late June at a different site within 1° latitude, implying marked variation in reproductive timing. In contrast, our results suggest a distinctly seasonal pattern of reproduction in Andean bears inhabiting dry tropical forest at Cerro Venado, Peru (6.4°S).

Table 1 Seasonal occurrence (delimited by the equinoxes and solstices) of births to captive Andean bears in the Northern and Southern Hemispheres in four latitudinal zones: Tropical ($\leq 23.5^\circ\text{N}$ or S), Low Temperate (23.5–35°N or S), Mid Temperate (35–55°N or S), and High Temperate (55–67°N or S)

| Latitudinal zone | Spring | Summer | Autumn | Winter | Total |
|------------------|--------|--------|--------|--------|-------|
| High Temperate | 0 | 0 | 0 | 8 | 8 |
| Mid Temperate | 3 | 4 | 43 | 218 | 268 |
| Low Temperate | 3 | 0 | 6 | 26 | 35 |
| Tropical | 4 | 12 | 29 | 11 | 56 |
| Total | 10 | 16 | 78 | 263 | 367 |

^aNumbers indicate captive Andean bear births in the Northern and Southern Hemispheres

All 12 litters of free-living Andean bears for which we estimated birthdates occurred in a 4-month period from June to October, corresponding to the austral winter and indicating that implantation occurred from April to August. In contrast, five birthdates for cubs first observed in their natal dens implied a narrower, 8-week birth period from mid-June to mid-August. A narrower estimate of the birth period is expected given a reduction in sample size from 12 to five, but may also indicate bias in our aging method, given that all seven birthdates assigned to litters first observed away from the den were earlier than five estimates for litters first observed at the den, which should be more accurate (Fig. 1). Such biases could arise due to variation in growth rate, nutrition or other factors, and potentially reduced by gathering repeat observations of mothers and cubs over time (Jongejan, Arcese & Sinclair, 1992). Nevertheless, our results indicate marked seasonality in reproductive behavior, physiology and birthdate in Andean bears inhabiting dry tropical forest (Table 1).

Interestingly, mating behaviors were only recorded during a comparatively brief 6-week period in December–January (Fig. 1). Higher temporal variation in birth as compared to mating period suggests that mating and implantation may be triggered by different cues. Such differences are possible via embryonic diapause (i.e. delayed implantation), reported for captive Andean bears (Dehnhard *et al.*, 2006) and other bear species (reviewed in Spady *et al.*, 2007). Variation in the timing of embryonic diapause, reactivation of corpora luteum, or implantation could be linked to environmental and/or internal cues, but have the effect of uncoupling the timing of birth and mating in ways that allow each activity to occur at the time of year likely to maximize individual fitness (Sandell, 1990).

Facultative seasonality in Andean bears

Our analysis of birthdates in captive Andean bears corroborates and extends those of Spady *et al.* (2007), who suggested that Andean bears adjust reproductive timing facultatively. We also observed an increase in the seasonality of births (i.e. less variation) in captive bears housed further from the Equator. That finding is consistent with the hypothesis that photoperiod will become more influential of reproductive timing in free-living Andean bears as latitude increases. In contrast, we expect photoperiod to have smaller effects on reproductive timing in Andean bears living nearer than further from the Equator, as shown in other long-lived mammals (Bradshaw & Holzapfel, 2007; Bronson, 2009). However, our finding that seasonality in reproduction declines close to the Equator suggests that Andean bears may lack the endogenous circannual rhythm typical of temperate-zone bear species that maintain seasonal patterns of reproduction at tropical latitudes (Spady *et al.*, 2007).

Phenotypic plasticity in reproduction

The timing of reproduction in captive Andean bears housed in the Tropics was more flexible than among captive bears housed at temperate latitudes. However, seasonality in the

reproduction of free-living Andean bears at Cerro Venado further suggests that bears inhabiting that region display behavioural and physiological plasticity linked to annual variation in climate, plant phenology and resource availability. The observed effect of photoperiod on reproduction in captive Andean bears at high latitudes may also imply that free-living bears at low latitudes may be constrained in their ability to adjust reproductive timing to resource availability as environments change (e.g. Visser *et al.*, 2010; Beever *et al.*, 2017).

In summary, we report marked seasonality in the reproductive timing of free-living Andean bears that inhabited tropical dry forest near the equator, where annual pulses in food abundance follow seasonal variation in climate but variation in photoperiod is low. In contrast, captive bears at tropical latitudes reproduced aseasonally, illustrating plasticity in behavior, and facultative as opposed to obligate seasonal reproduction. These findings imply that Andean bears have some capacity to adjust to temporal and spatial variation in resource limitation, and thus to accommodate climate-related shifts in plant phenology at tropical latitudes. However, if photoperiod constrains reproduction in free-living Andean bears at low latitudes, it may also constrain their ability to respond to climate-induced shifts in resource availability.

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