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MEDIA REVIEW

In it for the Long Haul: Impacts of Seasonality on Primates, Primatologists and Paleoanthropologists

Review of *Seasonality in Primates: Studies of Living and Extinct Human and Non-human Primates* by Diane K. Brockman and Carel P. van Schaik (Cambridge University Press, 590p., $130).

It's books like this that makes me envious of my wife's decision to become a paleontologist. Researchers in her field share a certain security that one can make strategically timed 4- to 6-week expeditions to collect fossils, and spend the rest of one's time in a lab, preparing and describing them. The timing of the field season can be dictated by comfort (e.g., avoiding the cyclone season), logistics and teaching schedules. In general, the fossils' relative lack of mobility means that those not collected in June will likely still be there in August.

Primatologists are less fortunate. Whether we choose to study diet, ranging, social dynamics, dispersal, nutrition, disease or almost any other aspect of primate life, our results will be almost certainly be affected by the season in which we head to the field. In fact, almost any ecological or behavioral question at the root of a study (e.g., ''how does x affect y?'') can be extended by adding ''and how does this vary with season?'' Although many established researchers and Ph.D. students get around the issue by studying their primates for a whole year or more, and explicitly examining the effects of seasonality, masters or undergraduate students, or professionals with other time commitments, must think carefully about how results can be affected by our choice of field schedules.

That said, evolutionary responses to the changing abiotic and biotic environments are emerging as fascinating and poorly understood parts of wild primates' overall survival strategy. In fact, rather than being an additional complication to original study questions, primates' responses to seasonality are increasingly becoming study questions in themselves. Additionally, the development of paleoclimatology has enabled researchers to reconstruct changes in climate (sometimes including seasonality), leading to various efforts to link past climate to evolutionary trends and innovations, especially in the lineage leading to modern humans. It is therefore fitting that an edited volume is dedicated to these two issues. Its goals, laid out by the editors in the first chapter are (1) to summarize and investigate how environmental seasonality affects resource availability for living primates, including humans, and the primates' various responses and (2) how these responses might inform our interpretation of evolutionary change in our hominin ancestors.

Sections 2 and 3 (extant habitats and their primates) span eight chapters and include a wide coverage of continents and taxonomic groups. Chapter 2 (van Schaik and Pfannes) provides a useful primer of tropical habitats, climate and phenology from a primate's point of view, covering the expected and observed seasonal variation in abiotic aspects of climate (temperature, insolation and rainfall) and the responses of the vegetation (peaks of flower, fruit and young leaf availability and their timing relative to one another). Hemingway and Bynum (Chapter 3) review published accounts of seasonality's effects on primate diet and ranging, summarizing 234 impressive studies covering 119 species. They find strong effects of region (continent), body mass, phylogenetic history and environmental seasonality on the nature and degree of responses. They conclude that behavioral shifts are crucial to primate survival through periods of low resource availability or quality: most primates change their diet, whereas only a few shift their range to track preferred foods across the landscape. The specific fallback foods, called keystone foods here, vary greatly, including exudates, nectar, flowers, fruit, seeds, leaves, pith and bark, but they share the fact that they are available yearround or when preferred resources are scarce.

Rasmussen (Chapter 4) illustrates an extreme example of seasonality's effects on behavioral ecology. She shows that two lemurs reduce their daytime activity and become more cathemeral during the dry season and argues that this constitutes an antipredator response (their deciduous habitat loses much of its leaf cover during this season, leaving primates more vulnerable to raptor predation). The mongoose lemur has smaller groups and body size than the brown lemur, and predictably exhibits the

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most extreme response. Schmid and Kappeler follow with another ''extreme'' example, reviewing the physiological and behavioral responses of nocturnal primates (mostly lemurs). This includes a timely summary of new research into torpor and hibernation unique to Cheirogaleidae, including detailed time records of circadian fluctuations in body temperature, ambient temperature and metabolic rate in wild animals. Most nocturnal primates reduce energy costs by having relatively low resting metabolic rates, especially during the day, but only Cheirogaleids exhibit torpor/hibernation and pronounced seasonal fat storage; why other groups have not converged upon these strategies remains unclear.

Alberts et al. (Chapter 6) use a 15-year data set to examine seasonal and interannual changes in Amboseli baboons. They identified behavioral consequences of using ''fallback'' foods in the dry season, including an increase in foraging time and a decrease in resting. However, these differences were smaller than those observed across years in response to changes in climate and vegetation, illustrating why it can be dangerous to judge seasonality based on a single year. This chapter might prove especially useful in reconstructing early hominin ecology, given that baboons are likely similar to our ancestors in their environment and ecology. Hill (Chapter 7) uses baboons to provide a useful glimpse into an understudied aspect of seasonality: the effect of day length across different seasons and latitudes. Primatologists are used to examining activity budgets in terms of percentages of available time, but it is easy to forget about the considerable variation that exists in the latter. This chapter shows that increasing day length makes it easier to avoid thermal stress—baboons with longer days rest in the shade more at mid-day because they can more easily re-schedule foraging to cooler times of day and still meet intake demands. This leads to important predictions regarding changes in activity and thermoregulation across seasons as well as across latitudinal gradients.

In Chapter 8, Mitani and Watts summarize the evidence for seasonality in non-human primate hunting. They find that hunting is seasonal for chimps at several sites, for capuchins at only one of two sites, and non-seasonal in baboons. Although it is tempting to offer primate hunting, especially that of chimps, as a model for early hominin hunting, the authors admirably resist this temptation. First, chimps don't use meat as a fallback food: hunting peaks during fruit-rich seasons, likely because these conditions allow the aggregations of males necessary for successful hunts. Second, primate-hunting methods (usually arboreal) contrast strongly with early hominin hunting (likely terrestrial). Third, meat is not a critical resource for any non-human primate, including the hunting champions, the Ngogo chimps; yet, it was likely obligatory at mid- to later stages of hominin evolution. Seasonality in human hunting is examined more directly in Chapter 9 (Bliege Bird and Bird), who studied the ''Martu'' aboriginals of western Australia. Hunting strategies varied by sex and season, as might be expected based on differing prey availability and differing currencies for obtaining social status between males and females. This provides an interesting starting point, but more studies across human cultures and regions will be necessary to develop generalities which can be used to infer behavior in extinct hominins.

The fourth section of the book shifts from the nuts and bolts of behavioral ecology to some of its transcendent properties: reproduction and social organization. First, Brockman and van Schaik (Chapter 10) provide a useful review of reproductive timing in extant primates. The ''capital-breeding'' vs. ''income-breeding'' dichotomy is explained and expanded—to include an intermediate category (''relaxed income breeding''). They end by examining the conditions that may have led to the different strategies, and provide behavioral and physiological predictions for different breeding strategies. To the extent that these predictions are testable given current data, the model is largely upheld.

This is followed by a review of primate birth seasonality (Chapter 11, Janson and Verdolin). This chapter should be required reading for any primatologist investigating seasonality, less for its results than for its extremely important appendix that introduces the use of circular statistics. Most past studies of birth seasonality fall in one of two categories. The first uses simple categorical statistics (e.g., χ^2 test) to examine the distribution of births across months. This is inappropriate because it treats each month as a separate, unordered category, thereby ignoring the closeness of adjacent months. The second uses an ordered but linear test such as the Kolmogorov–Smirnov test (months are ordered 1–12; e.g., January = 1, February = 2, etc.). This is more appropriate, but still assigns an arbitrary start and end: why should January be 1 and not June? Circular statistics are a more appropriate and sensitive approach, treating each month as one-twelfth of a circle and thus acknowledging the cyclical nature of seasonality. It sounds complicated but as the short appendix illustrates, its elegance is matched, thankfully, by its relative simplicity of application. The rest of the chapter is equally useful: Janson and Verdolin use this new technique to assess birth seasonality in 70 primate populations and use a meta-analysis to examine potential influences, explaining nearly two-thirds of the variation. They find an effect of latitude (likely acting via resource availability), as well as diet and body mass (these are interrelated but it appears that diet has a stronger independent effect), and continent (Madagascar's lemurs are always more seasonal than

expected). The timing of births relative to resource availability and the geographic distribution of birth seasonality are largely concordant with the income-capital continuum.

In Chapter 12, Knott examines energetic responses to food availability in our closest relatives, the great apes, and their implications for reproduction. She finds, in concordance with Chapter 3, that apes use a variety of fallback foods. However, the near starvation, inducing fat catabolism, and altered ranging seen in Bornean orangutans during non-mating years are linked to their use of lower-quality fallback foods (leaves, bark and pith) relative to chimpanzees and gorillas. In the next chapter, Ellison and colleagues review birth seasonality across living human cultures and the hypotheses proposed to explain its existence. They recognize that social factors (e.g., conception peaks around cultural holidays) and climatic factors play a role but propose that the effect of energetics is most important. Similar to other ''capital'' breeders, including great apes, humans have physiological mechanisms to increase the chances of conception when energy balance is higher. Finally, Plavcan et al. (Chapter 14) examine the effects of seasonality on sexual dimorphism (in canines and body mass) across primate species, considering both direct (e.g., seasonality's effects on ideal body size, via resource availability) and indirect pathways (e.g., via effects on social system and the monopolization potential of estrous females).

The following section examines another transcendent manifestation of behavioral ecology: community ecology. Van Schaik and colleagues (Chapter 15) expand on recent papers investigating determinants of primate species richness and biomass, finding that rainfall seasonality affects species richness in the neotropics and Madagascar, but the effect varies across regions and guilds. They also present an important new hypothesis for the surprising positive relationship between seasonality and folivore biomass in communities with colobines: higher rainfall seasonality causes greater deciduousness, causing leaves to grow faster, making them higher quality. For frugivores, there is a similar unique contribution: increasing frugivore biomass with increasing lag time between fruit and flush peaks suggests that the availability of young leaves when fruit is not available affects biomass more strongly than the fruit itself. Jablonski (Chapter 16) extends this community analysis into the past and examines primate diversity of four major primate groups across the Cenozoic in relation to paleoclimate and geography.

Had the book stopped at this point, I would have happily recommended it as a useful review of seasonality in primates and not felt anything missing. That the authors go further and tread into more uncertain waters gives this book the potential to make an even greater contribution. The final section, ''Seasonality and Human Evolution,'' examines what studies of seasonality in extant primates and humans can tell us about the ecology and evolution of our bipedal ancestors over the past 7 million years. Much has been made of the links between *climatic change*, especially cooling and drying trends, and the ''decision'' of our ape ancestors to become bipedal, hairless humans and subsequent changes. The important question here is does seasonality (*intra*-annual climatic variation) offer anything new to this debate?

Three chapters attempt to address this question. First, Reed and Fish (Chapter 17) review our current knowledge of the evolution and ecology of hominins (bipedal human ancestors) and link this with available knowledge of paleoclimate (of which there is a great deal) and paleoseasonality (of which there is much less; see below). Second, Kingston describes how the various eccentricities of earth's orbit lead to interannual variation in insolation, and therefore climate (''orbital forcing''). Finally, the co-editor Brockman steps in to review all previous chapters and summarize how far we have come in using extant primate and human seasonality to reconstruct past ecologies.

Sadly, the reader expecting an answer to this important question will inevitably be disappointed, for two reasons. First, the coverage given to this topic (three chapters) is extremely short relative to other sections, leaving the reader with a relatively unbalanced book. Second, and most importantly, it quickly becomes clear that we currently know extremely little about paleoseasonality, rendering the question somewhat premature. In an age where we are familiar with reconstructions of past temperature trends from such things as ice cores (think Al Gore's ''An Inconvenient Truth''), it is harder to imagine how to extract the *intra-annual* reconstructions of temperature, rainfall and food availability that would be needed to apply the lessons from extant primates. Some new developments hint toward improvement, such as a recent thesis examining the record of wetter and drier months recorded within fossil mollusk shells from Hadar, Ethiopia [Hailemichael, 1999], but we still know very little. This point is largely overlooked by this book's chapters on primate (Chapter 16) and human (Chapter 17) evolution, which tend to conflate aridification with increasing seasonality (one *may* be a proxy for the other, but if we use it as such, we can never determine their independent effects).

Although it is easy to imagine a primatologist appreciating this book as a resource outlining the ''state of the art'' in primate seasonality studies, its utility to a student of human evolution is harder to frame. It is incomplete as a manual in how to apply primate seasonality to the human fossil record, but perhaps useful in promoting an understanding of extant primate seasonality among paleoanthropologists,

thereby providing inspiration for coming breakthroughs in applying extant knowledge to extinct organisms.

In summary, even if this book's overarching question remains unanswered, it is at least better framed for a coming generation of study. In addition, the importance of the question is well illustrated: mounting evidence shows that myriad aspects of extant primate biology (diet, ranging, social behavior, community ecology, etc.) are shaped not just by overall climate, but by seasonal bottlenecks in resource availability. Thus, the most common foods (i.e., those that might figure most strongly in microwear or isotope-based dietary reconstructions for extinct species) might not be the most important foods in terms of limiting population density and driving evolutionary change [Lambert et al., 2004]. It seems, after all, that paleontologists *are* limited by seasonality—even if they can pick and choose the seasons when they go hunting for fossils; their understanding of the ecology of their once-extant study subjects is incomplete without understanding the massive selective forces generated not only by climatic change but also by potentially important ''lean'' seasons within those years.

References

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