Part I *Introduction*

1 Seasonality in primate ecology, reproduction, and life history: an overview

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Introduction

Seasonality refers to recurrent fluctuations that tend to have a period of one year. Seasonality in climate is a basic consequence of the tilt of the Earth's axis relative to its orbital plane (e.g. Pianka 1994). As a result, the position of the zenithal Sun (when it is directly overhead) varies through the year. It is directly overhead at 23.5° S on December 22 (winter solstice, in northern hemisphere terminology), then marches north, reaching the Equator on March 21 (equinox), moving on to the summer solstice on June 22 at 23.5° N, where it turns south again, passing the Equator on September 23 (another equinox) toward the winter solstice. The Sun's march affects not only sunshine but also other aspects of climate, such as windiness and rainfall. Hence, seasonality is felt around the globe.

This book is about the impact of seasonality on the lives of primates. Members of the order Primates are confined largely to the tropics, where they occupy a broad range of terrestrial habitats, although 90% of species live in tropical forest (Mittermeier 1988). Hence, our focus will be on seasonality in the tropics. In this region, seasonal variation in temperature is limited: temperature fluctuations over the 24-hour day exceed the range of monthly means and frosts are extremely rare (MacArthur 1972). Likewise, variation in day length, although present everywhere except right on the Equator, is limited. However,

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seasonal variations in rainfall and sunshine characterize all tropical habitats. Tropical climates are usually classified according to the duration and intensity of the dry season. By and large, seasonality increases as one moves from the Equator, i.e. with increasing latitude (see Chapter 2).

Animals respond to changing weather conditions in direct ways such as seeking shelter from rain or avoiding direct sunshine, but these direct responses tend to have only a limited and transient impact on their behavioral ecology. The major impact of climate is indirect. Climate is the fundamental dynamic force that shapes vegetation and in the long run affects soils. The indirect effects of climate come in two fundamentally different kinds: (i) the effects of climate on the phenology of the plant community, and thus on the abundance, nature, and distribution of potential food items, be they plant or animal, and on the amount of cover where plants are deciduous; and (ii) the effects of climate on the structure of the vegetation, from evergreen tall rainforest to sparsely covered open scrubland with virtually no woody vegetation. In this book, we will explore the impacts of these two distinct kinds of seasonality on the lives of primates, albeit with an emphasis on the first.

Humans are primates, and likewise have a tropical origin. Major events in hominin evolution have been ascribed to changes in seasonality (in this book, hominins are defined on the basis of an adaptive shift toward obligate bipedalism). Most hypotheses focus on the permanent effects of increased seasonality, such as the impact of forest fragmentation on the evolution of bipedalism and rates of speciation in the early to mid Pliocene Epoch (Foley 1993; Klein 1999), while others emphasize the role that fluctuating climates may have played in the appearance of stone tools and regular utilization of animal protein in early *Homo* (Potts 1998).

The aim of this book is to examine the impact of seasonality on the behavioral ecology, reproduction, social life, and life history of primates. The results of this analysis can then be used as a background against which to evaluate hypotheses proposed to explain aspects of hominin evolution. There are, as yet, few clear empirical generalizations on how primate range use, foraging, and reproduction respond to seasonality in resource abundance, and hence no clear explanations for the variability. Much of this book will therefore be devoted to documenting the main patterns in nature and developing hypotheses to explain them. In the rest of this introduction, we will develop the framework for this exercise.

Seasonality and behavioral ecology of primates

Activities

The majority of primates are diurnal and, once habituated, easy to observe. As a result, we have more detailed descriptive information on their activity budgets, range use, and reproduction than for any other mammalian order, and increasingly this information is also accumulating for the smaller and non-diurnal species. These studies have shown that primate behavioral ecology varies over time; in most cases, a seasonal signal in these fluctuations is clearly evident. However, although there is enough seasonal variation to warrant a synthetic examination of general patterns, there has until now been no attempt to develop a set of generalizations that can serve as a framework in which to interpret hominin behavioral ecology.

For example, primates are substrate-bound organisms that cannot undertake lengthy seasonal migrations to escape from periods with unfavorable conditions. Thus, some species appear to increase their activity during times of scarcity, whereas others decrease it, some even to the point of hibernation. At present, there is no good explanation for this variation. Likewise, whereas organisms with fast life histories can complete a full reproductive cycle during a seasonal peak in food abundance, primates, along with other long-lived organisms, with their long gestation and lactation periods, respond to seasonality either by coordinating peak demands of mid lactation with seasonal peaks in food abundance or by using those peaks to initiate a new reproductive cycle (van Schaik & van Noordwijk 1985). Thus, empirical patterns in how slow-breeding, Earth-bound tropical mammals respond to predictable seasonality in their natural habitats remain to be elucidated and explained.

Primates cue into and respond to various indicators of seasonality, particularly variations in the type and distribution of food. Most primates prefer ripe fruit with its readily assimilated energy. Fruit comes in discrete patches, as single fruit trees, lianas, or groves of interconnected plants. Abundant evidence indicates that primates do not cruise through their ranges in search of this food, but rather exploit their range based on continuously updated knowledge about the distribution of suitable patches (e.g. Garber 2000). Thus, temporal changes in the abundance of new plant organs (“phenology”), and the invertebrates dependent on them, will affect these consumers.

Optimal foraging theory (Stephens & Krebs 1986) predicts that as preferred food items become scarce, less preferred foods (fallback foods that have lower energy return per unit foraging time) will become included

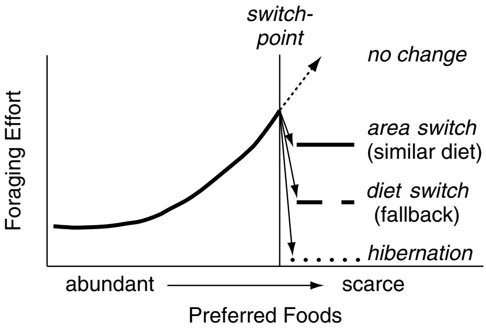

Figure 1.1 The possible responses to a decrease in the abundance of preferred foods, forcing animals to range more widely in order to maintain constant net energy intake. When foraging effort becomes too great to be maintained, animals can switch to different areas or different diets or hibernate.

in the diet and patches of food (e.g. fruit trees) will be more depleted before the forager moves on to the next patch (Charnov 1976). Most primates have a mixed foraging mode in which some foods are encountered as the animals move through their range, but most of the movement is driven by the need to exploit a known set of patches in a near-optimal order (e.g. Janson 2000). In the absence of a formal theory for predicting the response of primates to reductions in the preferred food types in such a foraging system, we can develop some qualitative expectations concerning the responses of consumers (Fig. 1.1). As preferred foods such as succulent fruits become more scarce, either because the patches become smaller or because the distance between them increases, the animals can continue to maintain a constant daily net energy intake by taking more fruit in each patch (perhaps by including less ripe fruit) and by traveling more, either visiting more patches or traveling longer distances between the same number of patches. However, as food abundance continues to decline, full compensation becomes increasingly difficult and net intake will begin to suffer.

Beyond the point of easy compensation for reduced availability of favored foods, animals can respond in a variety of ways (Fig. 1.1). The first, the *area switch*, involves a move into a different habitat that is phenologically out of synchrony with that currently occupied and where fruit abundance is higher. In this way, net energy intake can be maintained. Such a move, of course, requires that different habitats with out-of-phase fruiting peaks are available on a scale that is suitable for the consumers. Usually, this requires topographically complex landscapes, such as floodplains and uplands, valleys and hillsides, or mountain slopes of different exposures. We also expect to find this response in species that can easily

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travel over longer distances. Flying frugivores such as birds and bats therefore can afford to make the area switch much more easily, and should be more likely to remain specialized frugivores throughout the year, than substrate-bound animals such as primates.

A second response, the *diet switch*, should be more common among primates: the animals will switch to other foods, as predicted by diet breadth models, that produce lower return rates but require less travel to harvest. Examples include young or even mature leaves, unripe fruits, flowers, gum, and insects. Overall net intake on these fallback foods tends to be less because otherwise they would be used at all times (fallback foods also may be available during the period of high fruit abundance; see Chapter 3). Larger animals have lower energy requirements per unit body weight and therefore can afford more easily to switch to foods with lower energy density. Moreover, they have longer gastrointestinal systems, so more time is available to extract nutrients. For these reasons, it is expected that it will generally be easier for large animals, compared with small animals, to switch to a lower-quality diet.

The timing and extent of this diet switch may be affected by the fact that digestive efficiency of the fallback foods may depend on the cumulative intake over longer periods, perhaps because gut morphology and biochemistry become adjusted to them (e.g. Sibly 1981). Because energy intake declines when this switch occurs, we expect animals to reduce energy expenditure as well. This can be achieved because the fallback foods tend to be present at higher densities compared with the preferred foods, thus requiring less expenditure to harvest. Indeed, in some cases, animals may even lower their basal metabolic rates during the period of food scarcity (Pereira 1995). Among primates, this response may be especially common in lemurs, which may explain why many lemur diets are relatively less energy-dense than those of other primates of similar size and even why their reproductive seasonality is more pronounced (see Chapter 11).

Opportunities for diet switching may be more limited where the season of fruit scarcity is also one in which young leaves and organisms depending on them are scarce. There is a trend toward more positive covariation between the production of flush and fruit in areas with longer dry seasons, and independently in Neotropical forests (see Chapter 2). This pattern suggests that diet switches will be observed more commonly among larger species, among Paleotropical species, and among species in less seasonal habitats. Hemingway and Bynum (Chapter 3) demonstrate the importance of both area and diet switches in detail for non-human primates.

The third major response is found where the food situation becomes markedly unfavorable for a predictable period during the year. Animals can then dramatically reduce their requirements by hibernating in a safe place. Small animals consistently need high-quality foods. If they are also not highly mobile, we should therefore expect that smaller animals are more likely to hibernate, especially in the most seasonal environments and especially if they specialize on the most energy-dense foods, such as insects and fruits. Hibernation as a response to seasonal food stress is rare among primates and found only among small strepsirrhines (see Chapter 5), perhaps an extension of the reduced metabolic rate during the lean season.

Where hibernation is not an option, taxa may face a limit to the degree of tolerable seasonality. We should therefore expect to see a relationship between a species' body size and the degree of seasonality that it tolerates. Indeed, in Neotropical forests, smaller species may occur only in less seasonal forests (Cowlishaw & Dunbar 2000: 177), but van Schaik *et al.* (Chapter 15), who examine this more systematically, find little evidence for such a relationship. Within species, however, the response may go in the opposite direction, because smaller individuals need less food overall and therefore are more likely to survive the rigors of food seasonal scarcity. Plavcan *et al.* (Chapter 14) show that this expectation is generally met.

The classification of common responses laid out in Fig. 1.1 does not exhaust the possibilities. First, Alberts *et al.* (Chapter 6), studying baboons, describe a variant of the fallback foods they call *handoff foods*, where net intake remains approximately constant throughout the year in spite of a highly seasonal habitat and major diet switches. Bliege-Bird & Bird (Chapter 9) draw similar conclusions from their review of human foragers living in highly seasonal environments. Both cases suggest that intelligent omnivores might not face a lean season in the same way that regular consumers do, even in the face of severe seasonality in resource availability (see also Chapter 19). Second, some seasonal activities appear to have no direct relationship to seasonal food abundance. One possible reason is that the two sexes show different responses to seasonality, due to the different ways in which males and females maximize their fitness (see also Chapter 9). An example of this is hunting by chimpanzees, in which seasonally varying social conditions affect seasonal variation in hunting activity (see Chapter 8). Students of primate behavioral ecology face the challenge of predicting which of these many responses will be shown by particular species or populations.

Seasonality in cover and day length

Another environmental factor that can show dramatic seasonal variation is cover. In deciduous forest habitats, canopies go from bare to dense, and during the bare phase predation risk for smaller canopy species may be greatly increased. A few primates might respond to seasonal increases in vulnerability to predators due to bare crowns by hibernating (an issue not yet settled; see Chapter 5). Some others respond by changing their activity period. However, the majority will have to make more subtle behavioral adjustments to such dramatic seasonality in predation risk (see Chapter 4).

While it is easy to recognize the central roles that food and cover play in determining seasonal variation in activities, other seasonally entrained factors are also relevant. Especially toward the edge of the tropical region, day length can vary: for instance, at the tropics (23.5° N and S), the difference between maximum and minimum day length is almost three hours (Pianka 1994). Hence, even at constant food abundance, the daily duration of time available for foraging may create an apparent seasonality in food abundance, with its consequences for time budgets (see Chapter 7). Likewise, in open habitats (or in leafless forest canopies during the bare season), the absence of water and high daily maximum temperatures may lead to overheating unless special measures are taken. It turns out, perhaps remarkably, that only the first of these two environmental variables has a dramatic effect on primate range use (see Chapter 7).

Social life and life history

Fluctuating food abundance may affect social life in diverse, and sometimes counterintuitive, ways. Where declining abundance of preferred foods leads to fallback utilization of low-quality food items such as mature leaves, the nature of competition may change from a strong to a weak contest component and, hence, an increased scramble component (cf. Wrangham's [1980] "subsistence diet"). Thus, paradoxically, as food abundance declines, and competitiveness and aggression may be expected to rise, we may actually see an overall decline in rates of aggression. We may also see groups become less spatially cohesive.

Across a seasonality gradient within a species, or among a set of allopatric close relatives, we may see that group size declines, as a result of declining productivity, or increases, as a result of a gradient in diet composition toward lower-quality food but more abundantly available food items. Plavcan *et al.* (Chapter 14) show that both responses occur and no easy generalizations are possible.

Seasonality in climate, food, and reproduction may have subtle effects on the social life of a species that potentially affect demography and hence life history. In particular, seasonal reproduction could affect the operational sex

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ratio in primate groups, resulting in cascading affects on sexual dimorphism and other aspects of mating competition, male–female relations, and individual career trajectories (see Chapter 14). Overall, however, the impacts of seasonality on social behavior vary enough to prevent clear generalizations.

Seasonality and primate communities

Especially where severe, seasonality may limit the density of a species. Neotropical primates in seasonal forests were found to rely on only a few keystone resources to tide them over the season of fruit scarcity (Terborgh 1983). As a result, seasonality may affect both the species richness and the biomass of the local primate community. Other work, however, suggests that the main correlate of primate species richness is mean productivity (Ganzhorn *et al.* 1997; Kay *et al.* 1997), as expected by general diversity theory (Rosenzweig 1995). Van Schaik *et al.* (Chapter 15) find little evidence for an effect of seasonality on species richness. However, they do find that aspects of community biomass are predictably linked to seasonality.

Seasonality and reproduction in primates

So far, we have focused on coping with periods of resource scarcity, and animals may avoid reproducing during such periods. However, they may also be able to make use of periods of unusually high abundance of resources to reproduce. It is important to avoid the assumption that animals will attempt to maintain constant net energy intake, even though this is supported by numerous short-term laboratory experiments that varied food rewards per unit effort. In the wild, periods of positive energy balance will alternate with periods when energy losses are minimized. Hence, when food is most abundant, we may see animals work the hardest to gain a major energy surplus, used to support reproductive efforts, or in non-breeders to support growth or the buildup of energy stores in the form of body fat.

That animals such as primates, with slow reproduction involving long gestation periods and often even longer periods of infant dependence (Kappeler *et al.* 2003), respond to seasonal fluctuations in the availability of food with reproductive seasonality is not necessarily a trivial expectation. Seasonal reproduction will entail costs whenever the cycle is not an exact integer number of years, something especially likely to happen when

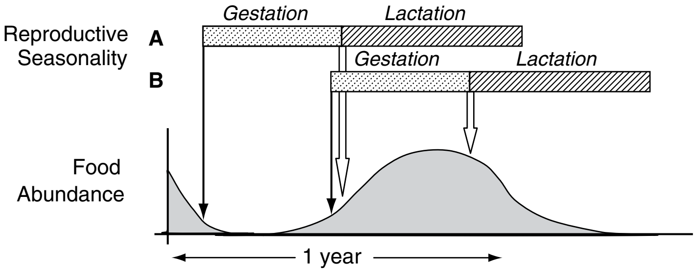

Figure 1.2 Two distinct modes of responding to seasonality in the abundance of preferred foods. In A, females are selected to give birth before the annual fruit peak and therefore have evolved sensitivities to exogenous cues that lead to conception one gestation period before this optimal timing (classic or income breeding). In B, females respond to increases in food abundance as cues for conception, leading to births one gestation period following that event, often coinciding with the end of the fruiting peak (alternative or capital breeding). ↓ approximate timing of conception; ⇩ approximate timing of birth. See Chapter 10 for further details.

infants die. The cost of the delay to resynchronize with the environmental cycle must therefore be outweighed by the benefit of increased prospects for growth of the infant or survival of the mother and/or the infant. Hence, there will be a threshold in resource seasonality below which no reproductive seasonality is expected (see Chapter 11).

In primates, the timing of reproduction relative to predictable seasonal fluctuations in resource abundance is not easy to predict (cf. Kiltie 1988). Figure 1.2 shows two possible reproductive responses. In A, the period of highest food (usually fruit) abundance coincides with the period of greatest energetic burden on the female, mid lactation. In B, increasing food abundance and the positive energy budgets associated with it are used to begin the reproductive cycle (van Schaik & van Noordwijk 1985). These differences are related to the difference between income (A) and capital (B) breeding (Jönsson 1997). Brockman & van Schaik (see Chapter 10) discuss both the proximate and the ultimate aspects of these two main response types, which produce contrasting temporal relationships between peaks in births and food. They show that the different response types vary in many features of their reproductive cycles, ranging from strict income breeding to relaxed income breeding to capital breeding. They propose the *Income–Capital Continuum Model* to accommodate this diversity of primate reproductive responses to seasonality, and test predictions of this model for primates, including humans.

A third response (C), no distinct seasonality at all, is of course also still a possibility. Surprisingly, in the same habitat, some species may show