

Characterization of primate environments through assessment of plant phenology

Andrew J. Marshall and Serge Wich

7.1 Introduction

Plant allocation to reproduction and growth is not evenly spread over time. In most plant species, production of flowers, fruits, and leaves is confined to a limited portion of the year (Leith 1974; van Schaik and Pfannes 2005). In some taxa, bouts of flowering, fruiting, and leaf flushing may be separated by periods of many years (e.g., Southeast Asian mast flowering and fruiting; Wich and van Schaik 2000). Plant phenological patterns create substantial temporal and spatial variation in the availability of plant foods and consequently primate diets, with a number of important implications for primate reproduction, grouping, ranging, and sociality (van Schaik *et al.* 1993; van Schaik and Brockman 2005). For example, in many primate species, reproduction is timed to coincide with periods when plant food availability maximizes the chances of offspring survival (Myers and Wright 1993; Knott 1998). The size and cohesiveness of primate groups often fluctuates substantially over time in response to the availability of plant foods (Chapman *et al.* 1995; Wrangham *et al.* 1996) and primate ranging patterns are often influenced by plant phenological patterns (Buij *et al.* 2002; Hemingway and Bynum 2005). Finally, fundamental differences in sociality among primate taxa are hypothesized to depend on the nature and temporal stability of a species' plant food supply (Wrangham 1980; Sterck *et al.* 1997; Marshall and Wrangham 2007). Accurate characterization of plant phenology is therefore centrally important to many facets of field primatology.

In this chapter we provide an overview of the methods primatologists employ to assess plant phenology. Our focus is on practical issues of most relevance to field primatologists who seek to characterize the environments that their study subjects inhabit. We discuss the benefits and limitations of various sampling methods,

selection of a sample to monitor, and the scale and scope of sampling. We end with a brief discussion of ways in which phenological data can be described, analyzed, and presented.

7.2 Field methods

Primatologists employ a range of methods to assess plant phenology. As with all decisions regarding sampling strategies, one must carefully consider the strengths and limitations of different methods, weigh various trade-offs (e.g., sampling intensively vs. extensively, financial and opportunity costs associated with allocation of time towards collection of phenology data), and select a method that is appropriate for the study to be conducted. For example, assessment of primate feeding selectivity and preference requires data on the availability of all potential foods in the environment (Leighton 1993; McConkey *et al.* 2002); research examining the behavioral or physiological response of a primate species to variation in its food supply can restrict sampling to known food plants for the primate species in question (e.g., Chapman and Chapman 1996; Knott 1998; Newton-Fischer *et al.* 2000); and studies of habitat use require simultaneous monitoring of plants across the full mosaic of habitats that the study population inhabits (Leighton and Leighton 1983).

Regardless of the method employed, a phenological sampling strategy should produce a description of a primate's environment that is accurate, precise, and representative. In this context, accuracy refers to the degree of conformity between the sample (e.g., the percentage of trees in plots bearing flowers in a particular month) and the actual value (e.g., the percentage of all trees within a focal primate group's range that are flowering that month). Phenological accuracy will increase with larger sample sizes of stems, greater numbers of independent sample replicates (e.g., more plots or phenology transects), and when sampling units are placed in an unbiased way (e.g., plots are randomly placed).

Precision refers to the amount of sampling error in measurements. Highly precise phenological sampling regimes will have low sampling error: repeat measurements of plant productivity at a given time, either by the same individual or multiple ones, will produce very similar results. Precision can be increased through adequate initial training of all who collect data, periodic cross-checks to ensure all involved researchers obtain concordant results, and use of clear protocols and unambiguous decision rules for field data collection.

Finally, phenological measures should be representative of the full range of environments that the target primate individual, group, or species encounters. Even when there is substantial spatial heterogeneity in a primate's environment,

representative results can be obtained via monitoring a large number of samples that are randomly located throughout the primate's habitat or by collection of data in a stratified manner that explicitly incorporates habitat variation into the sampling strategy (e.g., stratification of phenology plots based on forest type: Cannon *et al.* 2007b; Marshall *et al.* 2009a; Wich *et al.* 2011).

Here we focus on phenological methods appropriate for closed-canopy forests, as the majority of primates inhabit tropical or subtropical forests. Although we do not explicitly consider the assessment of plant phenology in woodlands, savannahs, or other environments, many of the principles discussed in this chapter apply to any primate habitat.

7.2.1 Selecting the sample to be monitored

All sampling methods have strengths and limitations, and some are better suited to particular studies than others (Table 7.1). Below we consider several methods and,

Table 7.1 *Comparison of phenological sampling methods discussed in the text.*

Sampling method	Description	Strengths	Limitations	Best suited for
Area based	Monitoring all plant stems that meet some basic criteria (e.g., size) within a delineated area (i.e., plot), usually multiple replicates are placed throughout the focal species' range	Unbiased, assuming randomly placed; stems sampled in proportion to their abundance; data can be used for other purposes, providing opportunities for collaboration	Time consuming; expensive; can provide too few stems of important, but rare, foods	Studies of unknown taxa or populations, where foreknowledge of diet is limited; studies that have a heavy ecological focus, where detailed description of plant phenology at the community level is necessary (e.g., preference studies)
Focal plant taxa	Monitoring a predetermined set of important food plants, often located along set phenology routes for easy access	Generally less work intensive; more efficient for some purposes as data are only gathered on species known to be food resources for the focal primate taxon	Requires foreknowledge of the species' diet in order to select target plant taxa; provides no information of habitat-wide productivity so can't assess	Studies of taxa for which long-term data exist, so it is relatively easy to determine which plant taxa are important to monitor; studies focusing on specific ecological

(continued)

Table 7.1 *Continued*

Sampling method	Description	Strengths	Limitations	Best suited for
			selectivity; stems are not monitored in proportion to their abundance, so difficult to place results in appropriate ecological context	interactions between primates and a particular set of plants (e.g., seed dispersal or predation studies)
Hybrid method	Use a representative number of plots to assess densities of all taxa, then monitor an additional set of rare but important taxa outside the plots. Then, in the analysis phase, be sure to scale the estimate of food availability by the stem densities	Provides unbiased sample of forest wide phenology and a more focused description of the food availability for the focal primate taxon	Difficult to know, <i>a priori</i> , how effort should be allocated among area-based versus focal taxon-based sampling	Collaborative studies with multiple researchers interested in different questions, so work can be divided up; forests that are not too spatially heterogeneous, so extrapolation from a limited sample is defensible
Fruit trails or traps	Walk along a predetermined route, counting fruits on the ground or placing traps of a standard size and periodically counting fruit fall into traps	Simple, replicable across sites; especially with traps, easily quantified and counted	“Only fallen fruits counted, fruits still in canopy not included; traps and fallen fruit can be disturbed by animals”	Simple cross-site comparisons (provided differences among sites that could bias comparisons are considered)
Remote sensing	Use spectral signatures of leaf flushing/fruit production	Broad spatial and temporal sampling; can sometimes be done retroactively, depending on imagery	Often imagery expensive, especially at high resolution; requires specialized training, skills; little taxonomic resolution; little information about understory	Very broad scale comparisons across space (and potentially time)

where applicable, illustrate our discussion with examples drawn from our own phenological studies in Indonesia.

7.2.1.1 Area-based sampling (e.g., plots)

Assessing plant phenology via area-based methods entails monitoring all plant stems that meet some basic criteria (e.g., diameter at breast height (DBH), height) within a delineated area (e.g., plot, transect). Plant stems in plots are normally permanently marked (e.g., with aluminum tree tags) and identified to the highest level of accuracy possible. Although desirable, perfect taxonomic identification is not required provided the confidence in botanical identifications is clearly reported and, for studies on primate diet, as long as the names used for plant stems in the plots match those used when gathering feeding data—even if the identifications are to morphospecies only. Usually, multiple sampling replicates are placed throughout the focal species' range, either randomly or by using a stratified random design that accounts for gross-level spatial heterogeneity (See Section 7.2.2). Provided they are accurately laid out and unbiased decision rules are made about inclusion of stems that fall on the edge of a plot, any shape can be used. We suggest, however, that the use of squares or rectangles is easiest and least prone to mistakes. In general, as mistaken determinations about whether or not to include stems that fall on the edge of a plot may bias results, we suggest minimizing the amount of plot edge for a given plot area (e.g., a 20 m \times 50 m plot is preferable to a 5 m \times 200 m plot as the former has roughly a third of the latter's perimeter).

When stems do fall on the edge of plots (e.g., when part of a tree's bole is inside the plot and part is outside), a clear decision rule must be created and consistently applied. In order to accurately sample the density of stems, the midpoint of the stem should be used to determine whether the plant falls inside or outside the plot (Fig. 7.1a). For example, if the plot edge passes through the bole of a tree with a 100 cm DBH in such a way that only 30 cm of the diameter is inside the plot, the stem should be excluded from the sample. Inclusion of trees that are less than halfway inside the plot would result in an overestimation of stem density, a bias that would be greater for larger sized trees (as large trees with midpoints that lie outside a plot are more likely than small trees to have part of their boles inside plots; Fig. 7.1b).

Lianas (woody climbers) present particular problems when establishing phenology plots. In addition to the challenge of determining the taxonomic identity of lianas, it is often difficult to determine which individual stems should be included and excluded from plots, and it is frequently difficult to determine the number of individual lianas present when lianas span multiple tree crowns. Although it is tempting to include in the sample any liana that enters the canopy of a tree inside a

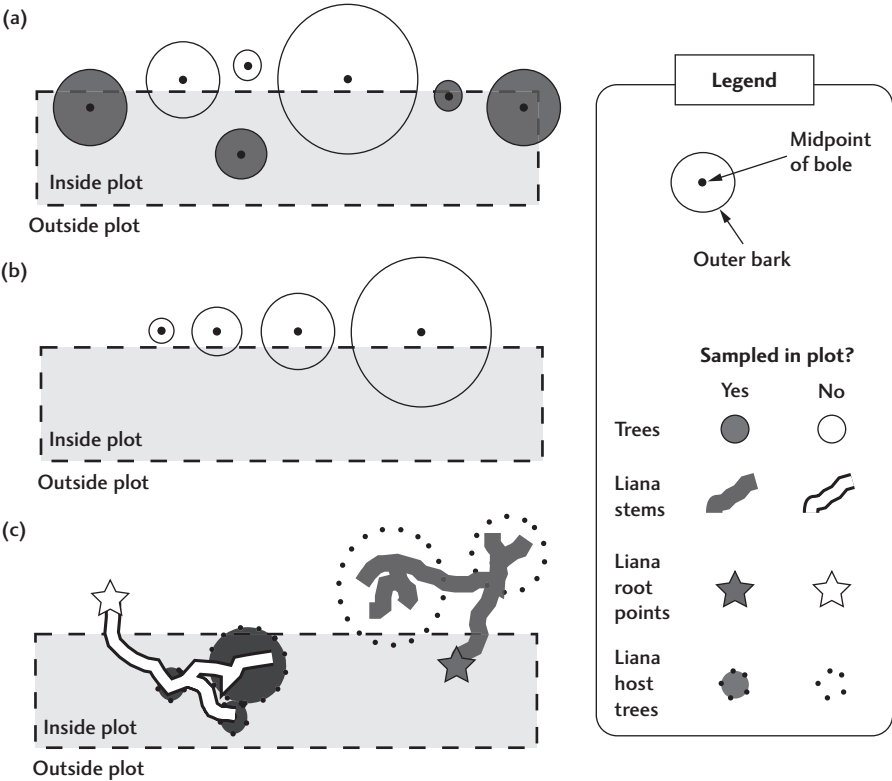


Fig. 7.1 Schematic depiction of phenology plots. The shaded region indicates the area inside plot, the heavy dashed line the edge of the plot. Circles depict stylized tree boles, with the midpoint of the stem indicated by a dot. (a) Trees whose midpoints are located inside the plot (shaded circles) are included in the sample; trees whose midpoints are outside the plot (open circles) are not sampled, even if a portion of their bole is located inside the plot. (b) Cartoon demonstration showing that the boles of larger trees are more likely to enter a plot than boles of smaller trees, although their midpoints are equally close to the plot border. This demonstrates why inclusion of trees based on whether any portion of the stem is found inside the plot biases estimates of stem density, a bias that is increasingly pronounced at large tree sizes. (c) Lianas should be sampled and monitored for phenology only when they are rooted (star) inside the plot (dark stem), regardless of which tree crowns they enter. Conversely, lianas rooted outside the plot (white stem) should not be included in the sample, irrespective of whether their host trees are sampled. Note that the size of the plot is not shown to scale relative to the size of the plant stems.

phenology plot, this method can lead to substantial biases since the inclusion of lianas in plots is then not directly related to their stem density. In order to obtain an accurate, unbiased measure of liana abundance and the phenology of lianas in a forest, we recommend including in the sample to be monitored only and all lianas that are rooted inside the perimeter of the plot. Thus, a stem rooted in the plot but which inhabits the canopy of a tree well outside the plot would be included, whereas a liana rooted outside the plot but which occupies a tree inside the plot would not (Fig. 7.1c). When a liana is rooted in multiple places, the last rooting point prior to ascending into the canopy should be used (Gerwing *et al.* 2006). This system requires knowledge of and clear marking of liana stems within the plot to ensure mistakes are not made in monthly observations. As epiphytes and hemi-epiphytes generally inhabit only a single tree, inclusion of individuals exhibiting one of these growth forms can be determined based on the location of its host tree.

Area-based methods provide a number of benefits. First, provided plots are placed randomly, they provide an unbiased sample of habitat-wide phenological patterns because stems are sampled in proportion to their abundance. Second, if one is beginning a primate study on an unstudied species or in a new environment, area-based methods are practical since they do not require foreknowledge of which plants are foods for the focal primate taxon. Third, these methods provide accurate data on the phenology of all potential foods in the forest, both things eaten and not eaten, permitting analysis of feeding selectivity. Finally, data from phenology plots are useful for a range of other questions. For example, subsampling of data permits assessment of temporal changes in food availability for any taxon in the forest for which dietary information is available (Marshall *et al.* 2009c).

Although providing the most comprehensive description of habitat-wide phenological patterns, area-based methods have considerable limitations. They are relatively time-consuming and expensive to establish and monitor (Chapman *et al.* 1994). For example, ongoing phenological work at the Cabang Panti Research Station (CPRS) in Gunung Palung National Park, West Kalimantan, Indonesia (Marshall 2009, 2010), comprising monthly monitoring of ten plots (totaling 1.5 ha) in each of seven forest types (roughly 6000 stems total), requires two full-time employees. In addition, since in many forests the majority of the effort spent conducting area-based sampling will be expended sampling non-food stems, and because many foods (especially preferred foods) are rare (Marshall and Wrangham 2007; Fig. 7.2a,b), area-based methods often produce sample sizes per food species that are inadequate for many types of analysis (i.e., fewer than 15 individuals per plant species, see section below).

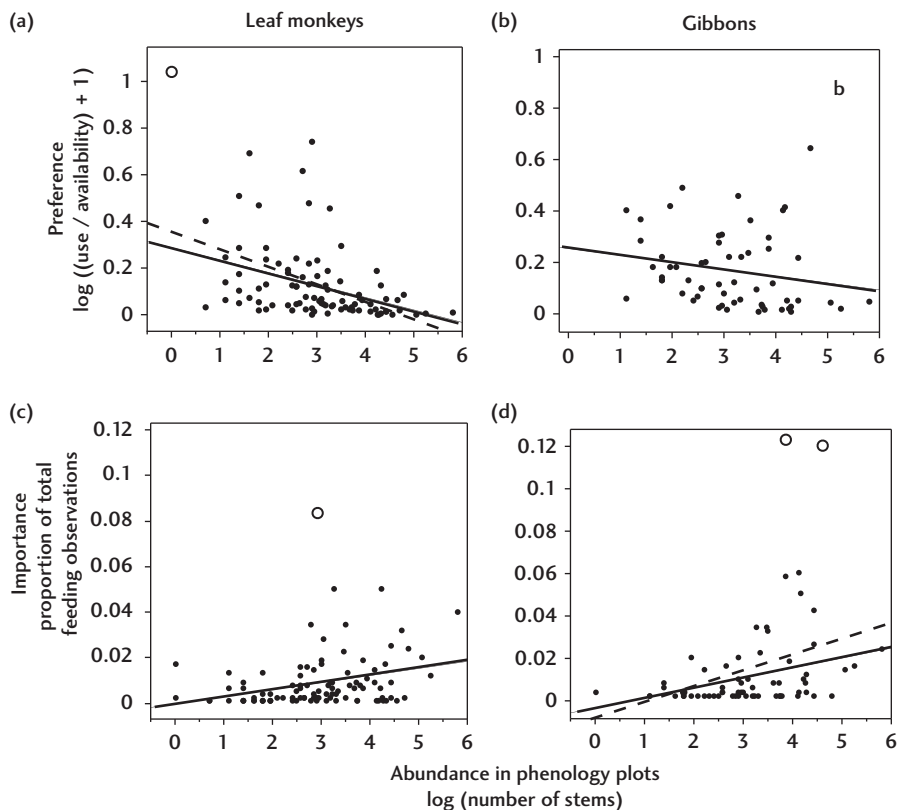


Fig. 7.2 Preferred foods are rare: (a) preference (use/availability) of leaf monkey food items ($\log(\text{preference} + 1)$) is negatively correlated with abundance ($\log(\# \text{ stems in phenology plots})$). Spearman's $\rho = -0.52$, $p < 0.0001$, $n = 89$ plant food taxa; when outlier in top left (the very rare *Adenanthera* (Fabaceae), open circle) is removed, results are consistent: $\rho = -0.50$, $p < 0.0001$, $n = 88$ taxa. Regression lines provided for visual clarity only (solid and dashed lines fit with the outlier excluded and included, respectively). (b) Same as panel a, but for gibbon foods. Spearman's $\rho = -0.32$, $p = 0.015$, $n = 58$ plant food taxa. Important foods are common: (c) importance (proportion of total independent feeding observations) is positively correlated with abundance (as in panel a). Spearman's $\rho = 0.35$, $p = 0.0005$, $n = 98$ taxa. Inclusion or exclusion of the highly important *Dialium* (Fabaceae, open circle) does not alter the results. (d) Same as panel c, but for gibbon foods. Including two highly important foods (both *Ficus* taxa (Moraceae) open circles) Spearman's $\rho = 0.41$, $p = 0.0005$, $n = 66$ taxa; excluding outliers, Spearman's $\rho = 0.38$, $p = 0.002$, $n = 64$ taxa. Regression lines provided for visual clarity only (solid and dashed lines fit with the outliers excluded and included, respectively). Preference, importance, and plant abundance data from Marshall (2004), Marshall and Leighton (2006), and Marshall *et al.* (2009b). Analyses include only the portion of the diet comprising fruit pulp and seeds. Samples sizes for leaf monkeys: $n = 734$ independent feeding observations; gibbons: $n = 481$ independent feeding observations. Plant data from 126 0.1 ha plots placed using a stratified random design across the seven forest types at CPRS ($n = 7288$ plant stems; Cannon *et al.* 2007b).

7.2.1.2 Sampling focal plant taxa

Primatologists frequently collect phenology data on only a limited, predetermined set of important food plants (Chapman *et al.* 1994). These stems are often located along set phenology routes and near existing trails for easy access. Generally, monitoring at least 5–10 stems of each species has been recommended (National Research Council 1981), although recent simulation analyses suggest that samples of 15 stems per taxon are necessary to adequately describe phenological patterns (Morellato *et al.* 2010). We note, however, that the target number may need to be larger, sometimes substantially so, to adequately address certain research questions (e.g., assessing the degree of phenological synchrony within a particular plant taxon) or where there is substantial spatial heterogeneity in the study system, when an adequate sample should be collected in each forest type. When using focal plant taxa to assess phenology, it is important that plants are correctly identified by experts to ensure the appropriate taxa are being monitored.

Plant species exhibit a broad range of complex sexual systems, including dioecy, where individual stems are either male or female (Croat 1979). When monitoring the phenology of dioecious species for the purposes of assessing fruit abundance, care must be taken to ensure that female individuals are selected because male stems never produce fruit (National Research Council 1981). Roughly 4–5% of the world's plant species are dioecious (Richards 1996), although the proportion of dioecious plants can be considerably higher in tropical forests. For example, it has been estimated that 26% of the tree species in Bukit Raya, Sarawak (Ashton 1969) and 21% of the trees and shrubs on Barro Colorado Island, Panama (Croat 1979) are dioecious; the proportion of stems that are dioecious seems to increase at larger tree sizes. As large trees are relatively rare in plots, ignoring the sex of sampled stems could introduce substantial error. Determining the sex of trees is usually impossible unless they are flowering, so for dioecious species, a larger number of stems should be monitored (e.g., ~30 stems per species) to ensure that an adequate number of female individuals are included.

Assessing phenology via study of focal plant taxa is popular among primatologists (e.g., Chapman and Chapman 1996; Newton-Fischer *et al.* 2000). In large part, this is because it is less time consuming than conducting comprehensive, area-based methods that require the establishment of plots. In addition, gathering data on solely focal food plants is an efficient way to measure temporal changes in the abundance of food, as time is not spent monitoring stems that primates do not consume. Although commonly used, the method does have substantial limitations (Chapman *et al.* 1994). First, this method requires foreknowledge of which plant taxa are important foods for the focal primate taxon, something that cannot be

known for an unstudied species or population. Even after years of long-term study, new food items are regularly added to the list of plants that a study group consumes (e.g., Rogers *et al.* 2004) making it difficult to be certain that all key foods are being monitored (Hemingway and Overdorff 1999). Second, as only known food plants are monitored, no information is available regarding availability of plants that are not food, meaning that assessment of feeding selectivity—which requires assessment of relative use and relative availability—is impossible (Leighton 1993; Marshall and Wrangham 2007). Third, as monitored trees are often clumped together along set phenology routes that are usually situated in convenient locations (e.g., near camp), they may not be representative of phenological patterns across the site, potentially biasing results, especially at large study sites. Fourth, as the number of monitored stems of a given plant food is not necessarily proportional to that food's importance in the diet (cf. Fig. 7.2c,d) or its relative abundance in the forest, measures of food availability derived from lists of focal plant taxa cannot be directly interpreted as indices of either the amount of food available for the target primate taxon or broader patterns of forest-wide fruit availability. Finally, these data cannot be used in most simple optimal foraging models, as these methods require habitat-wide measures of average food availability (Pyke *et al.* 1977).

7.2.1.3 A hybrid method

The two methods discussed above each have associated strengths and limitations. A hybrid of the two methods may be used that provides some of the benefits of each while limiting their attendant shortcomings. One form of this hybrid would be to establish a limited number of area-based plots to provide accurate, unbiased estimates of the stem densities of plants in the environment and to monitor their phenology. An additional set of relatively rare, but important food resources could then be tagged and monitored outside of the area-based plots to increase the sample sizes for these key resources. In the analysis phase, estimates of food availability from a particular plant taxon would be scaled by that plant's stem densities in the area-based plots. A second form would monitor only focal plant taxa (ideally across the full range of habitats that the study group or population occupies), as described in the previous section, but in the analysis phase data on plant productivity would be scaled by an objective index of habitat-specific abundance derived from botanical plots. These botanical plots would be surveyed once to determine floristic composition, but plant phenology would not be monitored in these plots. For an example of this approach see Willems *et al.* (2009). Assuming botanical plots provided an accurate and adequate sample of the entire range of the focal primate group or population (e.g., there are a sufficient number of replicates, the sampling

strategy is adequate to characterize spatial variation), both of these forms of hybrid method result in a phenological measure that provides an unbiased assessment of productivity while reducing (or eliminating) the amount of time spent sampling non-food plants.

7.2.2 Scale and scope of sampling

7.2.2.1 *Spatial scale*

Careful consideration of the spatial scale of the study is necessary to ensure that the phenology data collected are adequate to characterize the system. In general, as substantial spatial heterogeneity is common even within a forest type, multiple, randomly-placed replicates of smaller plots are generally preferable to a single, large plot encompassing the same sampling area (Hayek and Buzas 1997). If differences among habitat types that are relevant to the focal primate taxon or specific research question can be predetermined, stratified random samples are likely to be an efficient sampling strategy. In some cases, however, the delineations among habitat types of most relevance to the focal taxon may not be readily distinguishable at the start of a study; in these cases, random transect placement across the study area is most appropriate. The number of replicates placed will clearly be affected by the type of research question being posed and the availability of resources. We recommend that a minimum of 10 reasonably sized (e.g., ~ 0.1 ha) plots be used to characterize an area, be it a group's home range, a study area, or a forest type within a study area. In this context it is worth remembering that in some systems, contiguous forest types or home ranges can exhibit phenological patterns that are highly distinct, even to the point of being uncorrelated or negatively correlated with each other (Marshall and Leighton 2006; Cannon *et al.* 2007b; Marshall *et al.* 2009a; Wich *et al.* 2011). Sampling regimes that do not account for this source of variability or, at a minimum, permit the assessment of its potential magnitude, are not recommended.

7.2.2.2 *Temporal scope*

Determination of the temporal frequency at which to sample should be based on the goals of the study and knowledge of the phenological patterns of the species and plant parts in question. Although goals of primate field studies vary widely, and despite substantial variation in the duration of different phenophases (e.g., flowers are generally more ephemeral than fruits), most researchers default to sampling at monthly intervals (van Schaik and Pfannes 2005). As early as 1975, some argued that bi-weekly sampling was more appropriate for accurate characterization of tropical phenology because it would capture ephemeral events more accurately

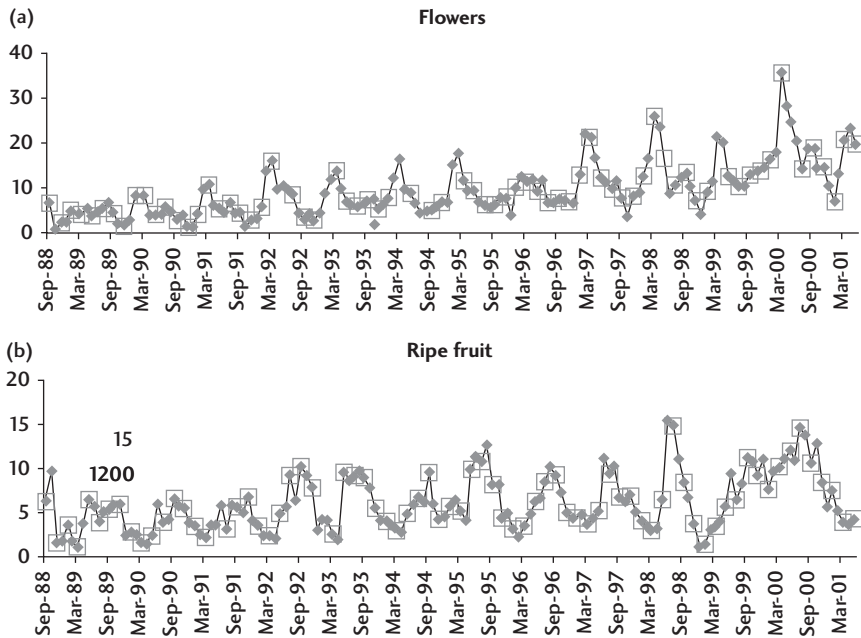


Fig. 7.3 Monthly (closed diamonds) and bi-monthly (open squares) percentage of trees carrying flowers (a) or ripe fruit (b) in the Ketambe study area. Data are from September 1988 until May 2001. Details on methods can be found in (Wich and van Schaik 2000).

(Fournier and Charpentier 1975). A recent study of specific plant species showed that sampling once a month or even at bi-weekly intervals missed flowering peaks and that therefore weekly measures better characterize the number of flowering events and the duration of flowering (Morellato *et al.* 2010). Analyses conducted at the community level show similar patterns: higher sampling frequency provides a more accurate picture of temporal variation (e.g., bi-weekly vs. monthly fruit trail counts: Chapman *et al.* 1994). There is, however, an obvious trade-off between sample size and sampling frequency. Assessing phenology on a weekly basis, as Morellato *et al.* (2010) advocate, would likely result in sampling of far fewer stems than is required to accurately characterize most primate foods (See Section 7.2.1.1), except in sites with extremely low floristic diversity. Sampling less frequently than once a month would permit monitoring of a larger number of stems, but could fail to record small, but potentially ecologically important, peaks in flowering and production of ripe fruit (e.g., Fig. 7.3a,b). On balance, monthly sampling is probably adequate for most primatological field studies, although researchers studying species for whom highly ephemeral resources (e.g., flowers) are important should consider sampling more frequently. A final consideration is the frequency of

primate sampling. For example, there is fairly limited utility in sampling plant phenology every other week if primates are only observed every other month.

Sampling duration is another consideration. Most researchers monitor phenology for the same period as they gather data on their focal primate species, which permits examination of the interactions between phenology and primate behavior for the duration of the study. In many areas, it is probably reasonable to interpret the results of a 2–3 year field study as indicative of the ecology of the system more generally—although this is unwise in regions where important phenological patterns occur on much longer timescales. For example, a field study of the duration of a typical Ph.D. project is unlikely to capture the full range of meaningful ecological variation in many Southeast Asian forests. At Gunung Palung, fruit production during mast fruiting events and during periods of low fruit availability can differ by more than an order of magnitude (Marshall and Leighton 2006; Cannon *et al.* 2007b). Periods of extreme food abundance or scarcity can last for extended periods, with important effects on primate physiology and behavior (Knott 1998; Marshall *et al.* 2009b). Short field studies of 1–3 years may well miss masts or the following periods of extreme fruit scarcity, meaning that only a subset of the full range of ecological variation experienced by most of the primate study subjects is sampled. Studies of limited duration also are inadequate to understand the reproductive biology of the plants themselves: in an intensive 5.5 year phenological study of more than 7000 plants at Gunung Palung, a large percentage of stems never reproduced during the sampling period (Cannon *et al.* 2007a).

7.2.3 Inclusion of various plant growth forms and sizes

7.2.3.1 Plant growth forms

Another consideration before establishing plots is which plant growth forms to include. Often, existing information about the basic biology of the study species will be helpful in making certain determinations. When studying primate taxa that never or very rarely go to the ground (e.g., Sumatran orangutans, gibbons), monitoring the phenology of ground vegetation is unnecessary. In contrast, some primates (e.g., gorillas, bonobos) feed extensively on terrestrial herbaceous vegetation, and phenological monitoring must therefore include adequate samples of these plants (Ganas *et al.* 2009). For arboreal species, often only trees are monitored in phenology plots. Lianas are very frequently excluded as they are difficult to identify and monitor and because determination of whether individual stems should be sampled is often time consuming (See Section 7.2.1.1). Nevertheless, lianas are important food resources for some primate species, especially during periods when trees are not fruiting (Leighton and Leighton 1983; Moscovice *et al.* 2007;

Marshall *et al.* 2009b). In such cases, exclusion of lianas from phenological samples results in an incomplete, and quite possibly inaccurate, characterization of food availability for the target primate species. For some primates, epiphytes can be key food resources (e.g., Irwin 2007)—in such instances they should be systematically sampled and monitored. Finally, as figs are extremely important resources for a variety of primate taxa, we strongly recommend sampling all growth forms of figs in phenology plots, including epiphytes, hemiepiphytes, trees, and lianas.

7.2.3.2 *Size cut-offs*

Ideally, samples used to monitor changes in food availability for a target primate species would include only stems of a size that the target species actually feeds upon. This would be desirable both because it would reduce time spent assessing stems that the target species never uses and because it would produce an index of food availability that was more accurately tailored to the primate species being studied. In practice, however, such information is not available at the beginning of a study and researchers instead must select an arbitrary cut-off below which plant stems are not sampled. Setting a size cut-off can be advisable for several reasons. First, there is an inverse relationship between stem size and stem abundance, so excluding small stems substantially reduces sampling effort. Second as small trees are more likely to be below the size at which trees start producing flowers and fruits, if your target primate species are frugivores, excluding them may not substantially influence the estimates of fruit availability you may be seeking. In the same vein, as there is a steep positive relationship between tree size and crop size (Leighton 1993; Chapman *et al.* 1994), exclusion of small trees that do produce fruit is unlikely to dramatically influence estimates of food availability in most cases. Of course, if your target primate species are folivores, it may be wise to retain even small stems in order to monitor leaf phenology.

A widely-used cut-off for trees is ≥ 10 cm DBH, which is a reasonable choice given the considerations listed above. (Note: breast height is generally taken to be 130 or 137 cm above the ground, although conventions are not universally followed.) Furthermore, use of the standard 10 cm DBH tree cut-off facilitates comparisons between sites (Marshall *et al.* 2009a; Wich *et al.* 2011). Lianas are less often measured by primatologists and size cut-offs used vary among studies. A published protocol for liana censuses advocates inclusion of all lianas with stems that are ≥ 1 cm in diameter 130 cm from the ground (Gerwing *et al.* 2006; Schnitzer *et al.* 2008); as with trees, the smaller the cut-off selected, the greater the sampling effort required. Liana crop size correlates positively with liana diameter (Marshall, unpublished data), but the relationship is fairly weak—meaning that it is less easy to be confident that exclusion of small lianas will not

have important effects on estimates of primate food abundance (cf. trees, previous paragraph). Finally, as hemiepiphytes can be extremely important food resources for primates in some forests (e.g., *Ficus* spp.), we suggest including in phenology samples all hemiepiphytes that are rooted in the ground, with at least one root with a diameter ≥ 1 cm, 130 cm from the ground.

Although most size cut-offs are reported as whole numbers and most DBH measurements are also recorded in the field as whole numbers (both in centimeters), care must be taken to ensure that the same rules for rounding are used in all plots. A generally accepted rule is that any measurement for which the tenths place is ≥ 0.5 is rounded up to the next whole number; measurements of < 0.5 are rounded down (e.g., 11.6 is recorded as 12, 11.4 is recorded as 11). Therefore, for example, if a DBH cutoff of ≥ 10 is used, the true cut-off should be ≥ 9.5 cm. If the cut-off used were actually ≥ 10 cm, then the first whole number category for DBH measurements would include only half the number of stems as the subsequent ones (e.g., stems measuring 10 to 10.49 cm would be included in the 10 cm DBH grouping, whereas for 11 cm DBH and groupings thereafter trees measuring 10.50 to 11.49 cm, etc. would be included).

As noted above, the use of a small size cut-off for trees is time consuming because small trees are very common. Therefore, for a given amount of sampling effort, the smaller the size cut-off used the smaller the area that can be sampled. Small sampling areas can result in phenology samples that may not be representative of the area to be sampled—particularly in the case of rare figs, lianas, and large trees that are often key food resources. One effective way to partially offset the trade-off between sample size and tree size is to use nested plots, in which small stems are monitored in only a subset of the plot. For example, Marshall and Leighton (2006) used nested plots to assess the stem density of gibbon and leaf monkey foods in each of seven forest types at CPRS, Gunung Palung. All fig roots and liana stems within 10 m on either side of the plot midline were included. The same rule was used for trees with DBH ≥ 34.5 cm. Trees with boles ≥ 14.5 cm and < 34.5 within 5 m of the plot midline were included. Thus, the sampling area for lianas, figs, and large trees that are often rare, important food sources was increased while limiting the time spent monitoring small, common trees. If data are collected using nested plots, care must be taken when calculating total stem densities because different sampling areas are used for different size classes.

An alternative to using a standard size cut-off for all stems is to tailor size cut-offs based on the plant taxon-specific minimum size at adulthood (i.e., the smallest size at which a plant bears flowers and fruit). Exclusion of non-reproductive individuals can produce a more accurate phenological estimate (e.g., if data are characterized as the percentage of stems with fruit) and reduce the amount of time spent

sampling immature stems. It is rare, however, that such data will be available, unless previous work at the same site was conducted prior to the beginning of a primate study. In addition, use of taxon-specific cut-offs requires a high degree of certainty about botanical identifications in phenology plots. Finally, its use severely limits the comparability of plot-level variables among studies. For these reasons, use of taxon-specific cut-offs will rarely be useful for primatologists establishing new phenology plots. In situations where monitoring of additional stems of rare but important plants is desirable (e.g., the hybrid method, Section 7.2.1.3), however, knowledge of the minimum size at adulthood can be very useful to ensure that the additional stems to be monitored have the potential to be reproductively active.

Regardless of the tree size cut-off used, care should be taken to establish and consistently apply systematic rules for situations where standard protocols are not applicable. Examples of such circumstances include when tree stems branch below breast height, where trees grow on slopes or have stilt roots or high buttresses, or when hemiepiphytes or lianas have multiple roots or stems. Discussion of every such eventuality is beyond the scope of this chapter, but forestry manuals and inventory protocols (e.g., Gerwing *et al.* 2006; Schnitzer *et al.* 2008) should be consulted in such circumstances and consistent rules applied.

Surprisingly few studies have, with hindsight after the study was completed, tested whether the size cut-off used for trees in the phenology plots accurately reflected the sizes of stems that the study species utilized. Wich *et al.* (2002) examined this for three species: Thomas langurs (*Presbytis thomasi*), long-tailed macaques (*Macaca fascicularis*), and Sumatra orangutans (*Pongo abelii*). For all three primate species the average DBH of trees fed upon was much larger than the size cut-offs in the phenology plots, but the minimum size of foraging trees was at or only slightly higher than the cut-off size (Wich *et al.* 2002). Thus, for these species, the size cut-off used (≥ 12.5 cm for trees) was appropriate, as it succeeded in capturing the phenology of all tree sizes fed upon while not overestimating food availability by using too low a size cut-off. We recommend that more such studies be conducted.

7.2.4 Characterizing the phenological phase

While patterns of plant growth and reproduction are, of course, continuous processes, generally primatologists use a limited number of discrete, visually-perceptible categories to classify the phenological phase of a plant stem (“Phenological development stages” *sensu* Brügger *et al.* 2003). Typically, the phenophases of flowers and fruits are assessed when present; often, new leaf flushing is also recorded. The precise categories used may vary between studies, but all methods

should be operationally defined, consistently applied, and clearly explained when results are reported. For example, Marshall and Leighton (2006) classified plants as reproductively inactive, or containing flower buds (i.e., visibly developing, but not at anthesis); mature flowers (i.e., at anthesis); immature fruits (i.e., fruits in which the seed is undeveloped); mature fruits (i.e., full-sized fruits that are unripe but have seeds that are fully developed and hardened); or ripe fruits (i.e., the final development stage prior to fruit fall, usually signaled by a change in color or softness). Other classification systems have simply recorded the presence or absence of fruit (e.g., Chapman *et al.* 1994; Newton-Fisher *et al.* 2000) or used a reduced number of categories to score phenophases (e.g., noted the presence of young leaves, flowers, or ripe fruit; van Schaik 1986). Frequently, a single plant stem may possess attributes of several phenological classifications concurrently (e.g., bearing a mixture of mature and ripe fruits). In such cases, consistent decision rules must be applied and incorporated into analyses so as not to “double-count” stems. One simple rule is to score the entire stem as the most advanced phenological stage present when the plant is observed (e.g., a plant bearing both flower buds and flowers would be scored as having flowers, Marshall and Leighton 2006).

Often, some specialized knowledge of the plant taxon is required to accurately assign a plant to a particular phenological phase, as, for example, it can be difficult to distinguish flower and leaf buds through binoculars or external cues may not reliably indicate ripeness (e.g., some *Dialium* spp. (Fabaceae), where immature fruits rapidly grow to full size and the seeds mature slowly inside the fruits over a period of many months with no visible external changes). When possible, it is therefore advisable to consult with knowledgeable botanists or others with experience at the study site to develop this knowledge. When this is not an option, we suggest observers take detailed, dated notes and photographs of phenological categories to check previous classifications once deeper knowledge of a plant taxon has been gained.

In addition to classifying the phenological stage of a stem, it is often desirable to assess a plant’s crop size. Crop size is measured in various ways: assessment of the proportion of the canopy bearing fruit, using a categorical scale, calculating crown volume, counting the number of fruits in the canopy, or by using DBH as a proxy (Chapman *et al.* 1992; Leighton 1993). Regardless of the method used, some assessment of the error and replicability of the estimate should be made, as the accuracy and precision of methods differ widely (Chapman *et al.* 1992). If such an assessment cannot be empirically made, then we suggest using an exponential scale that controls for the fact that for large crops estimates have disproportionately large associated errors (Leighton 1993). We note, however, that simple indices (e.g.,

percentage of stems bearing fruit) that do not incorporate crop size estimates are often adequate for many applications.

7.2.5 Alternative methods: fruit trails and litter traps

Two common alternative methods used to monitor phenology are fruit trails and litter traps. The fruit trail method entails an observer walking a predetermined route in the forest (often a clear trail so fruits can easily be observed) and counting the number of plant stems that have produced fruit that are encountered on the trail. Fruit availability is expressed as fruiting sources per km (Chapman *et al.* 1994; Buij *et al.* 2002). The litter trap method typically entails placing a number of square sheets of plastic or mesh of a standard size (e.g., 1 m²) on four poles that are stuck into the ground (e.g., van Schaik 1986; Chapman *et al.* 1994; Wright and Calderón 2006; Chave *et al.* 2010). At predetermined intervals (weekly, bi-weekly, or monthly) the material caught in the trap is collected and separated into leaves, flowers, fruit, branches, and others. These components are then counted or weighed. When counted, production can be measured as the raw or standardized number of items per unit time (e.g., seed production per year; Wright and Calderón 2006). When weighed, the wet weights of items of interest are recorded immediately; the dry weight is recorded after oven drying (e.g., Chapman *et al.* 1994). Litter trap data are then reported as weight/ha/year per item or in total (Chave *et al.* 2010).

Both fruit trail and litter trap methods are straightforward and simple. An added benefit of litter traps is that they provide quantitative estimates of forest productivity that can be compared easily across sites (Chave *et al.* 2010) and linked to factors such as soil fertility. Nevertheless, both methods have substantial disadvantages. A major shortcoming is that both methods assess what has fallen on the ground, not what is available in the canopy. This bias has several important consequences (Chapman *et al.* 1994). For example, fruit production as measured in litter traps is likely to be particularly underestimated during periods of fruit scarcity, when virtually all fruits are consumed in the canopy (Terborgh 1983). Similarly, litter traps are biased against preferred food items, as these generally are disproportionately targeted in the canopy. Small crops that are fully consumed in the canopy will be completely missed. In contrast, litter traps can be biased in favor of items that are aborted by trees or vines as a result of insect damage (Janzen 1983). An additional concern is that data could be biased due to items being directly removed from litter traps prior to measurement (e.g., by rodents or ungulates), although two studies suggest that the effects are not large (1–3% of fruits in the traps were removed: Chapman *et al.* 1994; Goldizen *et al.* 1988). Finally, a large number of traps are needed to obtain reliable values. Thus, the litter

trap method has the added disadvantage of being very time consuming. A relatively large number of traps are required to sample the habitat in an unbiased way (Chapman *et al.* 1994), and the emptying of traps and separation, drying, and weighing of fallen items is time consuming.

Many of these criticisms can also be levied against the fruit trail method, although this method uses a presence/absence measure to assess fruit productivity and is therefore not as sensitive to resulting biases in data as litter traps. Although fruit trails can be rapidly sampled and therefore provide an efficient (although biased) index of fruit availability, they do not provide reliable data on the availability of flowers or leaves, both of which can be important components of some primate diets. However, if one is exclusively interested in a quick-and-dirty measure of fruit abundance for a primate species, for instance due to limited time and staff, this method is better than no sampling at all. If such a method is employed, the above sources of bias should be considered and care must be taken in the interpretation of results.

The extent to which various phenological methods yield similar results and which method provides the most accurate assessment of plant phenology are important research questions. This issue has received limited empirical investigation (Chapman *et al.* 1994; Hemingway and Overdorff 1999; van Schaik 1986) and certainly deserves additional study, as the most appropriate method will likely vary based on the research question, the primate species being studied, and the forests being sampled.

7.2.6 Remote Sensing

Phenological studies are increasingly incorporating data gathered via satellite (e.g., Pettorelli *et al.* 2011). The most frequently used index is the normalized difference vegetation index (NDVI, also see Chapters 5 and 9), which correlates with photosynthetic activity (Myneni *et al.* 1995) and therefore provides a useful index of leaf production and leaf cover. Specific reproductive phenophases, such as flowering and fruiting, cannot be discerned in these satellite images. Thus far, the use of remotely sensed data in primatology has therefore been mainly restricted to analyses at large geographical scales, such as continents or regions, where for instance the mean NDVI index values of primate home ranges are compared to that of a larger reference area (Zinner *et al.* 2002). A recent study compared measures of NDVI at monthly intervals to measures of food availability (flowers, fruits, and seeds) in focal trees on the ground and reported a correspondence between monthly NDVI indices and the day journey length and level of terrestriality in the vervet monkey (*Cercopithecus aethiops*; Willems *et al.* 2009). However,

because the relationship was non-linear, the interpretation was not as straightforward as one might have hoped.

The benefit of using satellite imagery is that it permits broad spatial and temporal sampling and therefore provides researchers with the data necessary to examine periods prior to their own study or monitor areas beyond their own study site, provided the relationship between the NDVI index and food availability has been firmly established in the relevant forest types in the area. Another benefit is that NDVI data are freely available on various websites (e.g., <<http://glcf.umiacs.umd.edu/data/gimms>>), so once one learns the required analytical skills they can be readily applied. At present, NDVI data are not sufficiently accurate to permit monitoring of specific plant taxa (although other remote sensing techniques, such as high-resolution aerial photography, show promise in this domain; e.g., Jansen *et al.* 2008), therefore to date these data cannot be used to examine interactions between the phenology of certain food species and primate behavior. Another disadvantage is that such imagery does not provide information about the understory, thereby limiting its value for primate species that frequently forage beneath the main canopy. Nevertheless, remote sensing is a rapidly developing technology, and useful, novel applications are likely to be soon available that will extend our ability to monitor plant phenology and understand its effects on primate behavior and ecology.

7.2.7 Conservation drones

A promising new method for obtaining phenological data and NDVI data is the use of unmanned aerial vehicles (drones). Current technology and software allows for the development of low-cost drones (Koh and Wich 2012) that can be used to obtain high-resolution images that can potentially be very useful to monitor phenological activity and NDVI. Although the utility of this technology for phenological monitoring has yet to be tested, the technique could potentially allow for low-cost phenological monitoring over large areas.

7.3 Data considerations

7.3.1 Description and presentation of data

There are several ways to describe and present phenology data. The simplest is to report the mean and some measure of variance, although graphical presentation of data is especially helpful (Newstrom *et al.* 1994). Although more complex presentations may be required in some circumstances (e.g., Newstrom *et al.* 1994), often simple line or bar graphs that either present the monthly means or the raw values

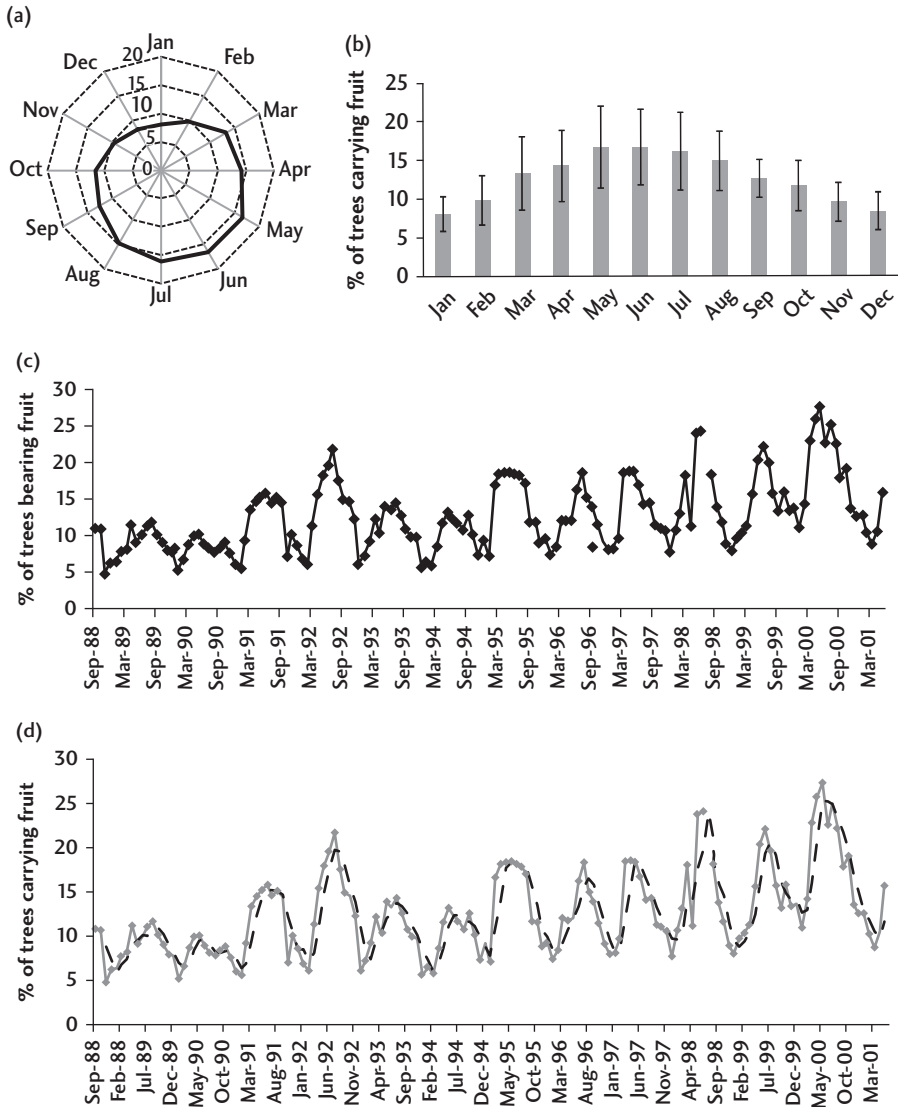


Fig. 7.4 Four different ways in which fruit availability can be presented, using data from Ketambe, Sumatra (Wich and van Schaik 2000). (a) As a circular figure where the mean percentage of fruit availability (black line) is depicted per month on a circle; (b) as a bar graph with the monthly means (gray bars) and standard deviations (black lines) across all years presented; (c) as monthly values connected with a line to show the time series; and (d) as monthly values as in 7.4c (solid gray line) with a three moving average plotted (black dashed line).

for all months (Fig. 7.4b,c) are adequate for primatological studies. Plots of moving averages are sometimes desirable, so that general cycles are clearly visible and short-term fluctuations (some of which may be the result of sampling error) are deemphasized (Fig. 7.4d). Although not commonly used to date (but see Janson and Verdolin 2005), circular plots (Fig. 7.4a) and circular statistics may be particularly applicable to phenology data (Morellato *et al.* 2010); they have recently been applied to large-scale comparisons of phenology data based on litter traps in South America (Chave *et al.* 2010).

Although it is common practice, we do not advocate calculating or presenting composite phenological indices that collapse, for example, measures of both fruit crop size and the number of stems in fruit into a single index. When such indices are used, the same value can be achieved by changes in either the number of stems or the crop size per stem. As the number and size of food resources are likely to have important, and often independent, effects, summing the two obscures important ecological variation of great interest to primatologists.

7.3.2 Modeling and hypothesis testing

Comprehensive discussion of methods for modeling phenological data and testing hypotheses within this framework is beyond the scope of this chapter. An excellent treatment of many related issues is provided in Hudson and Keatley (2010). Here we merely note two important considerations. First, phenology data sets generally exhibit substantial temporal autocorrelation (i.e., non-independent error variance). This error structure must be explicitly incorporated into models to avoid falsely inflating the significance of results. A variety of tools for time series analyses that permit incorporation of temporal autocorrelation are available, many as freely available packages in R (R Core Development Team 2011). Second, the types of phenological analyses likely to be most useful for primatologists entail using measures of plant productivity to predict outcome counts (e.g., feeding group sizes, numbers of animals encountered along transects) or proportions (e.g., the importance of items in the diet, activity budget measures). In such cases, assumptions required for most commonly applied statistical tests (e.g., OLS regression, t-tests), such as that variables are normally distributed, are normally invalid because data are, for example, counts with an abundance of zeros or proportions bounded between zero and one. In such cases Gaussian approximations are not appropriate and alternative distributions (e.g., Poisson, binomial, negative binomial) should be used in models designed to test hypotheses.

7.3.3 Applicability to studies of global climate change

Changes in atmospheric concentrations of greenhouse gases are likely to have a variety of effects on patterns of plant reproduction. Phenological studies are indispensable tools in documenting these effects (Chapman *et al.* 2005a; IPCC 2007; Hudson and Keatley 2010). Field primatologists have been monitoring long-term patterns of plant phenology at sites across the tropics, making them well placed to both detect the effects of global climate change on tropical plant phenology and to assess the cascading effects of these changes on populations of primates and other tropical vertebrates. Consideration of the nature of these changes and their possible effects is beyond the scope of this chapter, but two examples suggest how fundamentally important these interactions may be.

First, a long-term study in the neotropics has demonstrated that production of flowers and fruits is elevated during El Niño Southern Oscillation (ENSO) events and that there have been greater increases in flower production among sampled lianas than trees over the past two decades (Wright and Calderón 2006). Wright and Calderón (2006) suggest that documented shifts to more severe ENSO events, changes in atmospheric CO₂ concentrations, and increased solar irradiance may further alter patterns of flower and seed production, which are likely to have major effects on the abundances of forest vertebrates and alter tropical forest dynamics. Second, mast fruiting events in Southeast Asian forests are correlated with ENSO events (Curran and Leighton 2000; Wich and van Schaik 2000). ENSO years have been getting progressively drier in Southeast Asia over the past half century (Salafsky 1998), suggesting that the climatic trigger of mast fruiting may be intensifying. As masts have enormously important effects on many forest vertebrates (Curran and Leighton 2000; Cannon *et al.* 2007a), potential alteration or disruption of this system could have important and far-reaching implications. In both examples, it is impossible to predict the precise effects of such changes, but without long-term phenology data we will not be able to detect climate-induced changes, document their impacts on vertebrate populations, or devise potential mitigation strategies.

7.4 Conclusion

Primate diets vary substantially as a result of temporal and spatial variation in the availability of plant foods, with important implications for primate reproduction, grouping, ranging, and sociality. Many primatological field studies therefore require accurate characterization of plant phenology. Sampling methods have different strengths and limitations, so care must be taken to select the measure

most appropriate to the study species and the hypotheses to be tested. Regardless of the method employed, a phenological sampling strategy should produce a description of a primate's environment that is accurate, precise, and representative. In this review, we have aimed to summarize the major considerations related to the assessment of plant phenology by field primatologists and convey some simple rules of thumb that will facilitate the collection of high quality phenological data. We recognize that phenological data collection is often a relatively minor component of primate field studies, particularly in situations such as Ph.D. field studies when time and funds are severely limited. In such instances, while sampling intensity and methods may be less than ideal, we recommend that potential sources of error and bias be carefully considered. When suboptimal methods (e.g., fruit trails) are used, results must be interpreted with caution.

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