Seasonally Dry Tropical Forests

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Seasonally Dry Tropical Forest Mammals: Adaptations and Seasonal Patterns

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Seasonally dry tropical forests (SDTFs)—with a mean annual temperature greater than 17 degrees Celsius, rainfall ranging from 250 to 2000 millimeters annually and highly seasonal, and an annual ratio of potential evapotranspiration to precipitation of less than 1 (Holdridge 1967)—represent a unique combination of challenges for the living biota contained within them. The harsh abiotic factors create an environment that is hot, with little water, and that generally has an extremely variable but often sparse resource base. It is likely that both intra- and interspecific competition are greater in the severe environments encountered in SDTFs. As a consequence of these abiotic and biotic factors, many species that we think of as “tropical” cannot survive in the dry forest. Despite the biological, cultural, and long-standing economic interest in dry forests, these habitats and the mammals inhabiting them remain poorly known.

SDTFs represent some 42 percent of tropical ecosystems worldwide (Murphy and Lugo 1986a), yet only 14 percent of articles published on tropical environments in the last 60 years focus on dry forests (Sánchez-Azofeifa et al. 2005). This lack of research is changing rapidly, however. Of the more than 10,000 papers published on tropical ecosystems between 1998 and 2008, some 26 percent focus on dry forests (ISI Web of Knowledge, 1998–2008), but only 4 percent of these involve studies of mammals

($n = 103$). Recent research documents the great diversity and high number of endemic mammal species in SDTF (Ceballos and Navarro 1991; Ceballos and Garcia 1995; Stoner and Timm 2004; Ceballos and Oliva 2005; Timm and McClearn 2007; Timm et al. 2009).

A number of studies focus on adaptations of particular mammal species to seasonality in different environments (Fleming 1971b, 1977, 1988; Fleming et al. 1993); however, only a few papers attempt to review this theme at a broader level. Fautin (1946), in his classic study of the western Utah deserts, described the mammal community in this harsh environment, detailing adaptations that allow different species to persist in this strongly seasonal habitat. In reviewing the mammalian fauna in the SDTF along the Jalisco coast in western Mexico, Ceballos (1990) and Ceballos and Miranda (1986, 2000) present detailed ecological data, including adaptations for coping with seasonality. Similarly, the mammalian fauna and the ecology and adaptations for dealing with seasonality for dry forests in northwestern Costa Rica are summarized by Stoner and Timm (2004). In recent years, a wealth of studies published in widely scattered sources shed considerable light on the ecology of mammals in seasonally dry forests.

Herein, we review and synthesize the information that exists about the mechanisms of how mammals cope with and survive in SDTFs. Our emphasis is the Neotropics, but we also provide examples from other regions, focusing on unique adaptations to seasonally dry environments. We begin with a summary of the diverse array of physiological adaptations exhibited by mammals living in SDTFs. We then review behavioral adaptations utilized by mammals to cope with this harsh environment. We first describe the adaptation and then provide specific examples. We close each section by pointing out gaps in our knowledge and avenues for further research. We conclude with a discussion of the most serious threats to mammals found in SDTFs—forest destruction and fragmentation and the associated consequences of this threat to SDTF ecosystems.

Adaptations for Dealing with SDTF Environments

The mechanisms by which animals deal with extreme environmental conditions were perhaps best summarized by Fautin (1946, 295) in his classic study of the western Utah deserts:

The survival value of any organism is dependent on its physiological and morphological adaptation to the environmental conditions to

which it is subjected or to its ability to escape those conditions not favorable to its existence.

The primary challenges that mammals face in SDTF may be broadly divided into two basic groups: (1) physiological adaptations that allow animals not just to endure but to thrive in the environment and (2) behavioral adaptations that allow animals to seasonally escape the environment. Nevertheless, it is important to note that some behavioral adaptations (e.g., changing diet seasonally) require physiological adjustments, and thus behavioral and physiological adaptations are often intimately linked.

Physiological Adaptations

SDTF environments generally are characterized by high ambient temperatures and seasonal restrictions on the availability of water and food resources. Mammals living in these ecosystems must have adaptations not just to survive but also to reproduce. Several physiological adaptations to enhance survival and reproduction have been identified in mammals inhabiting dry forests that are similar to those found in desert environments, including daily changes in body temperature, seasonal torpor or hibernation, water conservation, and delayed reproduction.

CHANGES IN BODY TEMPERATURE

Body temperature (T_b) is the balance between heat production and heat dissipation and is relatively constant for an individual in most environments (Aschoff 1982). Nevertheless, T_b may undergo adjustments during the daily rhythm and be maintained at a lower average in hot environments, providing reduced energy expenditure and reduced water loss (Dawson 1955).

Lower body temperatures have been reported for several mammals inhabiting hot, dry climates, including marsupials (Lovegrove et al. 1999; Geiser et al. 2003; Warnecke et al. 2008), bats (Audet and Thomas 1997; Cruz-Neto and Abe 1997), primates (Fietz and Ganzhorn 1999; Schmid 2000), and rodents (McNab and Morrison 1963), and it is to be expected in armadillos. Day length may function as an anticipatory cue allowing the gray mouse lemur (*Microcebus murinus*; Cheirogaleidae) a mechanism to perceive upcoming environmental changes and adapt to them (Perret et al. 1998). More detailed studies with other mammals are needed to determine

which and to what extent environmental changes (e.g., day length, precipitation, temperature) may function as cues for adjusting T_b during the most critical times of year.

TORPOR AND HIBERNATION

Torpor is perhaps best defined as a state of reduced physiological activity usually accompanied by a reduction in body temperature, metabolic rate, respiration, and heart rate. Torpor that is short-term, for either part of a day or a few to several days, is referred to as daily torpor. Long-term winter torpor is referred to as hibernation and long-term summer torpor as estivation. Torpor and hibernation/estivation are best viewed as a continuum rather than discrete categories. Although torpor is most often described as an adaptive strategy to deal with cold weather (Lyman et al. 1982), whether of short duration (e.g., nighttime torpor) or long duration (hibernation), it is used by some mammals to deal with food shortage or large daily temperature fluctuations in seasonal environments, especially seasonally dry environments (Coburn and Geiser 1998; Kelm and Helversen 2007).

Diurnal torpor in tropical regions has been reported in blossom bats (Pteropodidae), leaf-nosed bats (Phyllostomidae), mouse lemurs (*Microcebus*), and dwarf lemurs (*Cheirogaleus*; Cheirogaleidae) (Audet and Thomas 1997; Bonaccorso and McNab 1997; Coburn and Geiser 1998; Schmid 2000; Dausmann et al. 2004). In the SDTF in northwestern Costa Rica, Audet and Thomas (1997) demonstrated that the short-tailed fruit bat (*Carollia perspicillata*; Phyllostomidae) and the little yellow-shouldered bat (*Sturnira lilium*; Phyllostomidae) frequently enter torpor while resting, depending upon their foraging success and body mass. Similarly, Kelm and Helversen (2007) document, under experimental conditions, that the long-tongued bat (*Glossophaga soricina*; Phyllostomidae) enters torpor under conditions of food restriction.

The most extreme cases of torpor in mammals are found in the species that hibernate. The best example of hibernation in SDTF is the Madagascar fat-tailed dwarf lemur (*Cheirogaleus medius*). Dwarf lemurs undergo true hibernation for nearly 6 months each year during the hot, dry season (Dausmann et al. 2004, 2005). Prior to hibernation, dwarf lemurs reduce their activity level and consume fruits high in sugars, resulting in an almost doubling of their body mass before entering hibernation (Fietz and Ganzhorn 1999), and as the common name suggests, fat is stored in the tail (incrassation). It is not clear why this phenomenon is unique to this

one primate species in Madagascar, given that a few to several species of primates occur in most dry forests, but we suspect that the small size of the dwarf lemur (130 grams), combined with the extreme seasonality of forests in which it is found (8-month dry season; average annual precipitation 800 millimeters), drove the evolution of this unique adaptation. This pattern of hibernation/estivation has not been described elsewhere for any Neotropical mammal in seasonally dry forests, but it might be a strategy used. The small South American arid-adapted, fat-tailed mouse opossums of the genus *Thylamys* (Didelphidae) may undergo a daily (diurnal) torpor, and they clearly store fat in the tail (Creighton and Gardner 2007). This species should be further investigated to determine whether hibernation/estivation occurs.

Most studies documenting torpor in SDTF mammals are recent. It is important to note, however, that many small-bodied mammals, including mouse opossums (*Marmosa*, Didelphidae) and pygmy skunks (*Spilogale*, Mephitidae), have not yet been adequately studied to determine whether they undergo torpor or fat storage. The possibility that torpor or even more-extended hibernation exists in other Neotropical mammals should not be ruled out until additional studies are undertaken.

WATER CONSERVATION

Given the high temperatures and extreme seasonality of rainfall found in tropical seasonal forests, water conservation is crucial to survival. Water conservation in hot, dry environments may be obtained through a variety of physiological mechanisms, including more-efficient kidney function, production of dry feces, concentrated urine, low evaporative water loss, and behavior. Although these adaptations exist in many mammal groups, they have been best studied in rodents. Some combination of these mechanisms is used by most heteromyid rodents that inhabit dry environments in the southwestern United States and western Mexico (Schmidt-Nielsen et al. 1948; Schmidt-Nielsen and Schmidt-Nielsen 1950). The extent to which they are developed is quite variable among species, however. Tracy and Walsberg (2001) suggested that evaporative water loss is the single most important trait associated with conserving water in Merriam's kangaroo rat (*Dipodomys merriami*; Heteromyidae). Fleming (1977) documented that the dry forest Salvin's spiny pocket mouse (*Liomys salvini*; Heteromyidae) tolerates greater weight and water reduction than the closely related wet forest spiny pocket mouse (*Heteromys desmarestianus*; Heteromyidae) and attributed these abilities to the fact that *Liomys* is found in a strongly seasonal environment. Hudson

and Rummel (1966) reported that the ability to occupy a burrow is the most critical adaptation for maintaining total water balance in *Liomys*. The importance of these mechanisms for water conservation in dry forest mammals has been inadequately explored; these and additional mechanisms almost surely will be found when they are more thoroughly studied.

REPRODUCTIVE DELAY

Physiological adaptations have been reported in SDTF mammals that enhance reproductive success in these harsh environments. Reproductive delays allowing parturition to occur when food resources are greatest have been suggested as an important physiological adaptation to deal with seasonality (Sandell 1990). Delayed reproduction may be divided in general into three main mechanisms: (1) delayed fertilization combined with sperm storage, (2) obligate delayed implantation, and (3) delayed development (Racey and Entwistle 2000). Delayed reproduction has been documented for more than 50 species of mammals representing 10 families (Sandell 1990); of these, 5 families—leaf-nosed bats (Phyllostomidae), flying foxes (Pteropodidae), armadillos (Dasypodidae), weasels (Mustelidae), and skunks (Mephitidae)—contain species that regularly inhabit SDTFs. With the exception of temperate bats, in which experimental work indicates that sperm storage may be for nearly 200 days (Racey 1982), sperm storage is not common in mammals and rarely exceeds a few days in length (Birkhead and Møller 1993; van der Merwe and Stirnemann 2007). Delayed implantation and delayed development, on the other hand, are better documented and may be widespread in SDTF mammals.

Reproductive delays in bats were first documented in north-temperate species that cope with short summers and long, harsh winters requiring the natal and lactation periods to coincide with the flush of insects appearing in the late spring and early summer. Having the period of mate selection and copulation, potentially expensive behaviors, coincide in late summer when food resources (and fat levels) are the highest may be critical to the reproductive cycle. Reproductive strategies in bats include sperm storage by the female after copulation, accompanied by the female's providing nourishment to the sperm, delayed implantation of the embryo, and delayed embryonic development (embryonic diapause). Reproductive delays are now documented in tropical bats inhabiting regions with long dry seasons (Bernard and Cumming 1997). Delayed embryonic development has been found in two of the most common Neotropical dry forest bats, the short-tailed fruit bat and the common fruit bat (*Artibeus*

jamaicensis; Phyllostomidae). Gestation in short-tailed fruit bats is approximately 4 months if delayed development is not employed, whereas gestation is 9 months when delayed embryonic development occurs (Fleming 1971a). Similarly, in the common fruit bat gestation is 113 to 119 days in nondelayed development, whereas it is 160 to 229 days when delayed development occurs (Wilson et al. 1991; Rasweiler and Badwaik 1997). In the seasonal forest of Barro Colorado Island, Panama, common fruit bats alternate episodes of normal embryonic development with delayed development, a pattern seen in no other bat (Wilson et al. 1991). In addition to delayed embryonic development, delayed implantation has been documented in the Paleotropical fruit bat *Eidolon helvum* (Pteropodidae) (Mutere 1967; Fayenuwo and Halstead 1974). All of the above-mentioned bat species are common in SDTFs, but they are not exclusive to this habitat. Very few species of bats in either the temperate or tropical regions breed throughout the year. The common vampire (*Desmodus rotundus*; Phyllostomidae) is one of the few species that is known to breed year-round, and this includes populations that occur in seasonally dry forests. Vampires that are located close to domestic livestock have essentially an unlimited food resource in the ready availability of blood and are thus able to breed irrespective of the climate.

The existence of reproductive delays in most mammals inhabiting SDTF has not been evaluated, and this phenomenon is undoubtedly more common than it appears. The proximate mechanisms responsible for the pattern of delayed reproduction observed are unknown; nevertheless, it is likely that seasonality of food and water resources may be important pressures affecting the evolution of these traits (Sandell 1990). The physiological mechanisms that control the processes of delayed development in mammals are very poorly known (Mead 1993) and represent an important avenue for future research.

Behavioral Adaptations

In addition to physiological adaptations, mammals that inhabit SDTF display a variety of behavioral adaptations that allow them to survive in these harsh environments. These adaptations allow animals to obtain sufficient resources, cope with the hot, dry environment, and reduce competition. Examples of these include changing diets, long-distance migration, short-distance migration, local movements, timing of activity and/or foraging, and seasonality of reproduction (Stoner and Timm 2004). As competition

is frequently more intense when fewer resources are available, animals in SDTF must cope with this as well.

DIETARY FLEXIBILITY

One of the most important environmental factors affecting the distribution and abundance of mammals is the availability of food (Peres 1997; Mendes Pontes 1999). The seasonality in rainfall, which is characteristic of SDTFs, results in considerable variation of resources at all trophic levels (vegetative and reproductive plant material, insects/invertebrates, and vertebrates) throughout the year (van Schaik et al. 1993). As a consequence, most mammals in SDTF are either dietary generalists that adapt and change diet as necessary or dietary specialists that move in and out of seasonally dry forests when resources are abundant or scarce (Stoner and Timm 2004).

The majority of seasonally dry forest mammals appear to be resident dietary generalists. Carnivores are one of the best examples of generalists in these habitats, and several studies document considerable variation in diet between seasons. The pygmy skunk (*Spilogale pygmaea*), for example—an endemic, threatened species found in seasonally dry forests in western Mexico—shows little overlap in diet between rainy and dry seasons. Pygmy skunks, which principally forage on invertebrates, incorporate a wider array of food items in their diet during the dry season (Cantú-Salazar et al. 2005). Similarly, the coyote (*Canis latrans*; Canidae), a generalist carnivore, shows considerable variation in diet between seasons both within and between sites (Vaughan and Rodríguez 1986; Hidalgo-Mihart et al. 2001). Other carnivorous/omnivorous species showing great dietary flexibility, as well as differences between seasons, include coatis (*Nasua*; Procyonidae: Valenzuela 1998; Alves-Costa et al. 2004), raccoons (*Procyon lotor*; Procyonidae: McFadden et al. 2006), and maned wolves (*Chrysocyon brachyurus*; Canidae: Bueno and Motta-Junior 2006).

Many species of frugivorous and nectarivorous bats exhibit considerable dietary flexibility in SDTFs. For example, Heithaus et al. (1975) show that several omnivorous and frugivorous species in the seasonally dry forest of Costa Rica adopt a diet almost exclusively of nectar and pollen during the peak of the dry season, explaining this phenomenon as an adaptation, not only to resource availability, but also as a way to increase water intake (i.e., from liquid nectar) during the driest time of year. Tschapka et al. (2008) document that the diet of the SDTF endemic long-nosed bat (*Musonycteris harrisoni*; Phyllostomidae) varies significantly between the dry and wet seasons along the Pacific coast of Colima, depending upon

resource availability. Dietary flexibility of bats is determined not only by resource availability but also by physiological requirements and limitations. The nectarivorous bat *Glossophaga soricina*, for example, meets its protein requirements by ingesting insects during most of the year in the seasonally dry forest of Chamela, western Mexico (Herrera et al. 2001). When *G. soricina* concentrates on plant parts, it obtains nitrogen from pollen (Herrera and Martínez del Río 1998). Other bats, such as the frugivorous *Carollia perspicillata*, have low metabolic requirements allowing them to survive on a low-nitrogen diet (Delorme and Thomas 1996), and they also consume insects at a rate that is more prevalent than was previously understood for frugivorous species based on studies of nitrogen isotope analyses of fur (York 2007).

Similar to bats, several rodents show considerable dietary flexibility in seasonally dry forests related to phenological changes and resource availability, with some showing significantly different gut morphology related to adaptations to particular diets. Seasonal differences in the size of digestive organs in caviomorph rodents in arid and semiarid habitats in Argentina occur as a consequence of variation in diet quality over seasons (Sassi et al. 2007). Similarly, an African savanna rodent community shows a gradient in gut structure allowing more granivory in some species than others and thus more dietary flexibility in seasonal environments (Kinahan and Pillay 2008). In sum, there is a complex interaction between behavioral and physiological adaptations that allows mammals in seasonal environments to cope with a changing resource base.

Several primate species found in SDTF also have flexible generalist diets. Capuchin monkeys (*Cebus*; Cebidae), for example, switch their diet to include more seeds and/or invertebrates during the dry season (Chapman 1987; Brown and Zunino 1990; Galetti and Pedroni 1994). Similarly, squirrel monkeys (*Saimiri*; Cebidae) consume more insects, flowers, and exudates during the dry season when less fruit is available (Stone 2007). Although howler monkeys (*Alouatta*; Atelidae) frequently are described as having one of the most flexible diets among Neotropical primates (Glander 1978, 1983), they are absent (Miranda 2002) or only found in low densities in the most extreme SDTF (Moura 2007). In spite of their apparent dietary flexibility, howler monkeys are quite selective in foraging on specific plants and ages of leaves, both daily and seasonally, in order to maximize total protein and essential amino acids and to minimize secondary plant compounds and fiber (Glander 1981, 1983).

Although much information exists about dietary flexibility of some mammals in seasonally dry forest, there is still a paucity of information

for most species. For example, published dietary information exists for the pygmy skunk from only one locality within its distribution in west central Mexico. Similarly, little quantitative information documents seasonal variation in diets of many phyllostomid bats, and the majority of studies focus on only a few of the most abundant frugivores and nectarivores. The extent of dietary flexibility in many small mammals in seasonally dry forest is still unknown, as basic diet information is just being documented for many species (Ceballos 1990). Finally, even in species that have dietary changes over seasons, how these may be affecting the physiology of the organisms has only been addressed for a few species of bats and rodents.

LOCAL MOVEMENTS AND LONG- AND SHORT-DISTANCE MIGRATIONS

Dietary specialists that consume a narrow range of items in their diet often cope with seasonally dry forests by shifting habitats within the forest or by migrating out of SDTFs. Spider monkeys (*Ateles*; Atelidae) appear to move seasonally, tracking availability of resources within seasonally dry forests as ripe fruits become less abundant (Stoner and Timm 2004). This highly frugivorous species does not switch its diet, as many SDTF mammals do, but rather invests more time in procuring ripe fruit resources (Wallace 2005). The abundance of many frugivorous and nectarivorous bats also varies seasonally within SDTF, suggesting that they move to different habitats within or adjacent to SDTF that provide more resources (Herrera 1997; Timm and LaVal 2000; Stoner 2001, 2002; Stoner et al. 2002; LaVal 2004a; Stoner and Timm 2004; Timm and McClearn 2007; Tschapka et al. 2008).

Local movements frequently involve the exploitation of riparian habitats within seasonally dry forests or adjacent higher altitudinal areas that contain more resources. For example, in the SDTF of Brazil's Caatinga region, howler monkeys are more common in canyons than cliff habitats during the dry season, probably because more tree species retain their leaves in this more humid environment (Moura 2007). In seasonal environments, both collared peccaries (*Pecari tajacu*; Tayassuidae) and white-lipped peccaries (*Tayassu pecari*; Tayassuidae) travel great distances, tracking resources and exploiting specific microhabitats that contain more food (Mandujano 1999; Stoner and Timm 2004; Mendes Pontes and Chivers 2007).

Long-distance migrations have been well documented for populations of the nectarivorous lesser long-nosed bat (*Leptonycteris curasoae*; Phyllostomidae). Each spring, long-nosed bats migrate from Mexico to the southwestern United States where they congregate in extremely large maternity

colonies. The young are born in caves that have high humidity and a stable thermal environment; after the young are fully volant, the entire colony returns to Mexico, usually in August (Hayward and Cockrum 1971). This migration follows closely the availability of several species of cactus and agave flowers that constitute critical food resources (Howell 1979; Cockrum 1991; Fleming et al. 1993). In seasonally dry forests along the western coast of Mexico, the lowest density of *L. curasoae* coincides with the greatest scarcity of chiropterophilic resources (Stoner et al. 2003). Rojas-Martínez et al. (1999) show that only populations north of 30 degrees follow this migration pattern, whereas the more southern populations consist of year-round residents. They attribute this pattern to the greater availability of resources year-round for the more southern resident populations. A similar pattern is observed in the insectivorous Mexican free-tailed bat (*Tadarida brasiliensis*; Molossidae). Free-tailed bats migrate in the spring from Mexico to the southwestern United States, form maternity colonies, and return southward in October (Cockrum 1969). The migrations are thought to be closely linked to the seasonal availability of preferred food items (Lee and McCracken 2005).

Seasonal migrations of nectarivorous bats of the arid United States and western Mexico are seen only in the larger species, whereas the smallest nectarivorous bats are permanent residents. Thus, body size, and presumably the ability to store energy during migration movements, may be a critical factor in allowing some species to migrate out of an area (von Helversen and Winter 2003). Conversely, or perhaps concomitantly, the evolution of smaller body size in nectarivorous bats might be an adaptation allowing these species to occupy areas that experience seasonal food shortages by reducing caloric requirements.

Several conclusions about mammal movements within seasonally dry forests are made by indirect evidence (e.g., absence or lower density during part of year). The true extent to which local movements to adjacent habitats occur for many mammalian species inhabiting SDTF is unknown. More detailed studies involving both telemetry data and indices of resource availability for particular species would be useful in evaluating the extent and frequency of mammal movements to surrounding habitats.

ACTIVITY PATTERNS

Adjusting activity patterns, in terms of both distance covered during the day and timing of activity, also represent an important behavioral adaptation allowing mammals to adjust to SDTF conditions. Some mammals

increase their home range during the dry season when food is scarce, to increase the search area for food, whereas others reduce their ranging patterns, perhaps to conserve energy. During the dry season, home ranges in white-nosed coatis are twice as large as during the rainy season, and their daily path is longer (Valenzuela and Ceballos 2000), presumably because they need to forage farther to obtain sufficient resources. Similarly, white-lipped peccaries expand their home range and foraging area when resources are scarce in tropical humid areas (Fragoso 1998), and they likely follow a similar pattern in areas of seasonally dry forests (Stoner and Timm 2004).

Large carnivores also show seasonal variation in their ranging patterns; however, they show a different pattern than the midsized mammals. Pumas (*Puma concolor*; Felidae) and jaguars (*Panthera onca*; Felidae) have significantly larger home ranges during the rainy season in SDTF along the coast of Jalisco than during the dry season (Núñez Pérez 2006). Presumably this occurs because prey is concentrated in higher densities around water sources during the dry season, whereas prey is more dispersed and found in lower densities during the rainy season. This same pattern has been described for leopard cats (*Prionailurus bengalensis*; Felidae) in dry forests in Thailand (Rabinowitz 1990).

In contrast, some primates utilize the strategy of energy conservation rather than foraging greater distances during periods of scarce resources in the dry season. For example, Verreaux's sifakas (*Propithecus verreauxi*; Indridae) in SDTF in Madagascar significantly reduce home range, core area, and daily path length during the dry season. Additionally, they display a daily period of inactivity during the dry season as a strategy to conserve energy (Norscia et al. 2006). Rodents also employ a strategy of foraging in smaller areas during periods of lower resources. Tomes' spiny rats (*Proechimys semispinosus*; Echimyidae), for example, in seasonally dry forests in Panama have larger and greater overlap of home ranges in the rainy season compared with the dry season (Gliwicz 1984).

Several mammals in seasonally dry forests are crepuscular or nocturnal, allowing them to escape high ambient temperatures during the day. Both jaguars and pumas are more active at night or early morning in the SDTF of Chamela (Núñez Pérez 2006). Other carnivores that are primarily nocturnal or crepuscular include civets (*Viverra*; Viverridae: Rabinowitz 1991), crab-eating foxes (*Cerdocyon*; Canidae: Vieira and Port 2007), and leopard cats (*Prionailurus bengalensis*; Felidae: Grassman et al. 2005). Several dry forest ungulates are principally nocturnal or most active in the early morning, including brocket deer (*Mazama*; Cervidae: Rivero et al. 2005) and Baird's tapir (*Tapirus bairdii*; Tapiridae: Foerster and Vaughan 2002).

Another technique for adjusting activity to cope with seasonally dry environments is to remain underground during the day, as found in many fossorial rodents, or remain underground continuously, as seen in many of the mole-rats (Bathyergidae), especially the naked mole-rat (*Heterocephalus glaber*: Burda et al. 2000) and silvery mole-rat (*Heliophobius argenteocinereus*: Galliard Šklíba et al. 2007). In spite of being encompassed in a relatively constant environment, the subterranean silvery mole-rat adjusts daily and seasonal activity based on small temperature fluctuations in the burrow, being less active in the dry season when resources are less abundant (Šklíba et al. 2007).

SEASONALITY OF REPRODUCTION

Most mammals, whether in tropical, temperate, or arctic regions, synchronize parturition to coincide with periods of greater resources (Clutton-Brock et al. 1989). Mammals found within seasonal tropical forests are especially sensitive to timing birth with food availability, since lactation is the most energetically costly activity of the reproductive cycle (Dall and Boyd 2004; Korine et al. 2004). In particular, many mammals that inhabit dry regions show clear patterns of birth related to seasonality and thus resource abundance. The physiological mechanisms by which mammals achieve reproductive delays are discussed above (see Reproductive Delay). Here, we present information about the seasonality of reproduction.

Most rodents that inhabit seasonal forests show strongly seasonal reproduction. In strongly seasonal forests in Panama, Tome's spiny rats give birth to young at the end of the dry season, presumably allowing lactating females and developing young to obtain more resources at the beginning of the rainy season (Gliwicz 1984). A similar pattern is observed in northwestern Costa Rica for Salvin's spiny pocket mouse, whose reproduction is seasonal, with young being born at the beginning of the rainy season (Fleming 1974; Janzen and Hallwachs 1996). Similar seasonality of reproduction has been described for rodents and small marsupials in the dry region of the Cerrado (Mares and Ernest 1995) and in the SDTF of Chamela (Ceballos 1995). Reproduction also has been linked to seasonal availability of food resources in several species of African rodents in the family Muridae that inhabit extremely seasonal forests, including Stella hylomyscus (*Hylomyscus stella*), Peters's hybomys (*Hybomys univittatus*), smokey heimyscus (*Heimyscus fumosus*), praomys (*Praomys* cf. *misonnei*), and Percival's spiny mouse (*Acomys percivali*) (Neal 1984; Nicolas and Colyn 2003).

Seasonality of reproduction in tropical bats was first documented

more than 70 years ago (Baker and Baker 1936; Baker 1938) and subsequently has been confirmed by many other studies (see Wilson 1979, Racey 1982, and Racey and Entwistle 2000 for reviews). In the Neotropics, bimodal polyestry is the most common pattern of reproduction in several families, including Emballonuridae, Hipposideridae, Megadermatidae, Nycteridae, Pteropodidae, and Rhinolophidae (Bernard and Cumming 1997; Heideman and Utzurrum 2003). Bimodal polyestry also is common in many Neotropical leaf-nosed bats (family Phyllostomidae) that inhabit seasonal tropical forests, especially frugivores and nectarivores (Fleming et al. 1972; Wilson 1979; Stoner et al. 2003). The timing of parturition is such that lactation coincides with greatest resource availability in seasonal forests (Timm and Lewis 1991; Bumrungsri et al. 2007). Although specific timing may vary between sites, usually parturition occurs at the beginning and middle of the rainy season, coinciding with greatest resource abundance for both frugivorous and nectarivorous bats (Bernard and Cumming 1997). Wilson (1979) associated the weaning of young in polyestrous species with the beginning of the rainy season, a period of maximal food abundance. Seasonal births during the beginning of the rainy season, however, have been seen in insectivorous bats in the Neotropics, including both of the families Vespertilionidae (van der Merwe and Stirnemann 2007) and Mormoopidae (Stoner et al. 2003). Bernard and Cumming (1997) suggested that weaning of young is a more important factor than the energetic costs of lactation in affecting the seasonality of reproduction in both frugivorous flying foxes and insectivorous bats in Africa, documenting that weaning is closely correlated with peaks in both fruit abundance and insect abundance.

In a comprehensive review of Neotropical primates, Di Bitetti and Janson (2000) documented that most New World monkeys studied so far show some seasonality in parturition. Nevertheless, several ecological and life history characteristics appear to affect the strength of the birth peak within species. In particular, they suggest that diet, body size, and latitude are all important factors that influence seasonality of births in Neotropical primates. Frugivores, for example, have more seasonality in births than folivores, larger primates are more seasonal than smaller ones, and primates farther from the equator show more seasonality in births than those closer to the equator. Additionally, parturition is timed to allow peak lactation (small-sized species) or weaning (large-sized species) to occur at a time of greatest resources. A recent study on captive brown capuchin monkeys (*Cebus apella*) comparing births in zoos over a latitudinal gradient concluded that brown capuchins breed seasonally, regardless of latitude and

constant food provisioning (Bicca-Marques and Gomes 2005). They suggest that latitude and the associated change of photoperiod, as well as food availability, are not important factors affecting seasonality of birth for this species. The black and gold howler monkey (*Alouatta caraya*) in northern Argentina, however, shows facultative behavioral response in timing births to coincide with greatest food availability (Kowalewski and Zunino 2004). We can conclude that significant variation exists in reproductive timing both between and within species of Neotropical primates and that further research is needed to identify both the proximate and ultimate causes of this variation.

Seasonal births also have been well documented for several species of lemurs in Madagascar in seasonal tropical forests. For example, Verreaux's sifakas give birth when resources are scarce at the end of the dry season but wean when resources are greatest at the end of the rainy season (Lewis and Kappeler 2005; Randrianambinina et al. 2007). Similar patterns have been recognized in several other lemurs in seasonal environments, including the black lemur (*Eulemur macaco macaco*; Lemuridae: Bayart and Simmen 2005), red-fronted brown lemur (*Eulemur fulvus rufus*; Lemuridae: Ostner et al. 2002), Milne-Edwards's sportive lemur (*Lepilemur edwardsi*; Lemuridae: Randrianambinina et al. 2007), and gray mouse lemur (*Microcebus murinus*; Perret 1992).

Although seasonal births have been documented for many of the species described above, few studies have documented the proximate mechanisms that allow the seasonality of reproduction to occur. Future investigations should evaluate variation in timing of reproduction for species that are found in more- and less-seasonal habitats.

Forest Destruction and Fragmentation

The most serious problem confronting tropical mammals today is habitat destruction from human activities and the resulting fragmentation that occurs with human disturbance (Stoner and Timm 2004; Timm et al. 2009). Largely as a result of being the most accessible tropical habitat for human colonization (see chap. 14), SDTF has been and is continuing to be destroyed at alarming rates worldwide—the last 50 years has seen the loss of most of the world's dry forests (Stott 1990; Steininger et al. 2001; Quesada and Stoner 2004; Sánchez-Azofeifa et al. 2005 and chap. 3; Miles et al. 2006).

In addition to lowering species diversity for most mammal groups,

forest destruction and fragmentation directly impact particular mammal species in several ways. First, forest destruction often results in range reductions, especially for large-bodied animals that require large expanses of continuous forest and for dietary specialists that require large foraging areas to obtain food resources. Consequently, range reductions may ultimately cause local or regional extirpation/extinction simply by eliminating essential habitat. Forest destruction also may affect mammal communities by providing the opportunity for a few generalist mammals to expand their populations in disturbed areas, thus resulting in greater population densities of particular species and sometimes increased competition both within and among species. Additionally, fragmentation and the consequent human colonization that commonly follows increase exposure of wildlife to hunting pressure (Cullen et al. 2000; Peres and Lake 2003; Reyna-Hurtado and Tanner 2005). Population dynamics and management of wildlife are critical issues in seasonal dry forests, and hunting, often illegal, continues to have a negative impact on both the mammals and forest structure (Dirzo and Miranda 1991). Examples of forest fragmentation and its impact on mammals in SDTF are discussed below.

Range Reduction and Species Extirpation/Extinction

Range reduction occurs as a consequence of habitat fragmentation for those species that have large home range requirements. Large and some mid-sized mammals are particularly susceptible to the negative effects of habitat fragmentation because of their habitat requirements (Redford and Robinson 1991; Dalecky et al. 2002; Ibáñez et al. 2002; Mendes Pontes 2004; da Silva and Mendes Pontes 2008). Different foraging guilds of large and mid-sized mammals may suffer the negative affects of range reduction in fragmented landscapes, including carnivores, herbivores, and frugivores.

Several studies have shown that large and mid-sized carnivores suffer from range reductions as a consequence of forest fragmentation (Chiarello 1999; Laidlaw 2000; Asquith and Mejía-Chang 2005). Home ranges of jaguars in the SDTF of Jalisco's Chamela-Cuixmala Biosphere Reserve are considerably smaller than those found in the dry regions of Parque Nacional Kaa-Iya del Gran Chaco in Bolivia (Maffei et al. 2004; Núñez Pérez 2006). These differences are likely attributable to the greater size of the protected area in Bolivia (34,400 square kilometers) versus Chamela (13,142 square kilometers) and the greater habitat fragmentation found within the

immediate area surrounding Mexico's biosphere reserve. Large carnivores, such as jaguars and pumas, are always among the first species to disappear from highly fragmented landscapes (Chiarello 1999; Laidlaw 2000; Asquith and Mejía-Chang 2005; Timm et al. 2009).

Forest fragmentation generally has a negative impact on populations of large and medium herbivores (but see discussion about elephants below) by reducing the availability of habitat and by increasing their susceptibility to hunting as fragmentation brings animals closer to human settlements (Cullen et al. 2000). Large grazing herbivores that have been particularly affected by fragmentation in dry regions in the Paleotropics include mountain gazelles (*Gazella gazella gazella*; Bovidae: Manor and Saltz 2004), Nubian ibex (*Capra nubiana*; Bovidae: Attum 2007), blue duiker (*Philantomba monticola*; Bovidae: Lawes et al. 2000), and African elephant (*Loxodonta africana*; Elephantidae: van Aarde et al. 2006). In Neotropical dry regions, several medium and large herbivores are suffering the consequences of fragmentation and the subsequent reduction in range, including tapirs (*Tapirus*), collared and white-lipped peccaries, and brocket deer (Chiarello 1999; Galetti et al. 2001; Ibáñez et al. 2002). In the seasonal forest of southeastern Brazil there is a direct relationship between fragment size and mammal species diversity—the largest species drop out of the smallest fragments first, explaining much of the lower diversity observed in small fragments (Chiarello 1999).

Large and medium terrestrial and arboreal frugivores are extremely susceptible to forest fragmentation and show smaller populations in smaller-sized fragments; these include agoutis (*Dasyprocta*; Dasyproctidae), pacas (*Cuniculus paca*; Cuniculidae), and spider monkeys (*Ateles*) (Chiarello 1999). In addition, the negative effect of forest fragmentation is exacerbated by hunting, which is frequently more common in forest fragments with adjacent human populations (Cullen et al. 2000). In a meta-analysis using an array of tropical habitats, Harcourt and Doherty (2005) show a universal negative effect of forest fragmentation on primates. Specifically, in Neotropical seasonal forests, several studies document that frugivorous primates, in particular, are not found in smaller forest fragments (Chiarello 1999, 2003). As their ranges become restricted by forest fragmentation, density is reduced, and then populations disappear within the smaller fragments.

In addition to large and medium-sized mammals, one group of smaller-sized mammals that frequently is affected by habitat fragmentation in tropical dry regions is bats. Since bats are volant and often have considerably larger home ranges compared with similarly sized terrestrial

mammals, they may suffer the consequences of reduced range caused by habitat fragmentation. For example, several studies in SDTF show that bat species diversity is lower in fragmented or disturbed areas and that some species are completely absent (Stoner et al. 2002; Quesada et al. 2003, 2004; Gorresen and Willig 2004; Timm and McClearn 2007; Ávila Cabadilla et al. 2009).

Increase in Species in Disturbed Habitats

Some mammals thrive in altered environments and actually increase in abundance in fragmented areas. For example, several generalist species such as common opossums (*Didelphis*; Didelphidae), coyotes, raccoons, and coatis frequently are found in higher densities in areas of human disturbance (Hidalgo-Mihart et al. 2001; Stoner and Timm 2004). In South Africa, elephants frequently increase in density as a result of fragmentation because regions are cut off that formerly represented routes of movement between different areas. This results in unusually high densities in fragments, and elephants can cause considerable property and habitat damage, often resulting in their removal by humans (van Aarde et al. 2006).

Competition has been identified as an important element of mammal communities living in SDTFs, since seasonality characterizes limited resources during part of the year. Increased densities in fragmented habitats will result in greater competition between similar species that are already competing in this harsh environment. For example, the low density and small group size of howlers in the dry region of the Caatinga is attributed to their competition with capuchins (Zunino et al. 2001). Gray and red brocket deer (*Mazama*) achieve niche separation by segregating through space and time along Bolivia's Chaco-Cerrado border. In the dry region of Brazil's Cerrado, crab-eating foxes (*Cerdocyon thous*) and the pampas fox (*Lycalopex gymnocercus*; Canidae) forage in different habitats and have different peak activity times (Vieira and Port 2007). Niche partitioning of two bovids (*Boselaphus tragocamelus* and *Gazella bennettii*; Bovidae) and two cervids (*Axis axis* and *Cervus unicolor*; Cervidae) in dry regions of western India is achieved by selection of different habitats; the cervids prefer forest habitats, whereas the bovids are found primarily in scrub lands and are more tolerant to disturbance (Bagchi et al. 2003).

The one "dietary specialist" that has increased its abundance manyfold with the increase in disturbed habitats is the common vampire bat. *Des-*

modus rotundus, an obligate blood feeder. It is the dietary generalist of the vampires and uses an extremely wide array of mammals, birds, and even reptiles as food sources. Clearly part of the increase in abundance can be attributable to the introduction by humans of domestic livestock, a ready source of easily obtained food for vampires.

In sum, there is no doubt that habitat fragmentation and forest destruction are having severe consequences on both the structure and the composition of mammal communities in dry forest regions throughout the tropics. The implications of changes in mammal communities for regeneration and forest structure and composition are discussed below.

Consequences of Lower Mammal Diversity in SDTFs

Range reductions of particular species, lower abundance, extirpation, extinction, and increased competition in altered human environments are having severe negative consequences on both the structure and the composition of mammal communities in dry regions throughout the tropics. Given the importance of mammals in biotic interactions such as seed dispersal (Howe and Smallwood 1982; Lobo et al. 2009) and pollination (Ghazoul 2005) in tropical environments, changes in their distribution and abundance may have severe consequences for SDTF ecosystems.

Mammals are one of the most important vertebrate groups that disperse seeds in tropical forests (Jordano 2001); in particular, primates (Lambert and Chapman 2005) and bats (Lobo et al. 2009) are recognized as the most important mammalian dispersers. The Central American spider monkey (*Ateles geoffroyi*) consumes and potentially disperses as many as 40 species in some SDTFs (González-Zamora et al. 2009). LaVal (2004b) reported that bats disperse more seeds than do birds, that pioneer species of plants are especially well represented in bat-dispersed seeds, and that these seeds are dispersed primarily to disturbed areas. Bats, because of their high mobility, can disperse large numbers of seeds for considerable distances. Altered mammal communities and the subsequent change in seed dispersal may have cascading effects and ultimately change SDTF plant species structure and composition and affect the natural process of regeneration within these ecosystems (Stoner, Riba-Hernández et al. 2007; Stoner, Vulinec et al. 2007).

In addition to their seed dispersal, mammals are important in tropical ecosystems also as external vectors for moving pollen (Ghazoul 2005). Bats are undoubtedly the most important mammal group responsible for pollination in tropical forests. Bats visit and presumably pollinate

more than 590 plants in the Neotropics and 160 in the Paleotropics (Winter and Helversen 2001). Pollination of chiropterophilic plants in seasonally dry forests differs in fragmented environments, which generally receive fewer bat visits and have consequent lower reproductive success (Stoner et al. 2002; Quesada, Stoner, Rosas-Guerro et al. 2003; Quesada, Stoner, Lobo et al. 2004; Arias-Cóyotl et al. 2006; Quesada, Sánchez, Azofeifa et al. 2009a). The ultimate long-term effects of this lowered reproductive success for plant community structure and composition are unknown.

Conclusions and Future Research

Dry forests originally were believed to be less diverse than wet forests, but recent research is documenting that some dry forests are as diverse as wet forests (see chap. 1 for a case of plant diversity). A wealth of excellent research has been conducted on mammals in the SDTFs, and this is especially true for the last decade. However, we must emphasize how much remains to be learned about dry forest mammals, how they function in their environment, and how critical it is to continue and expand studies as dry forests continue to disappear and the surrounding buffer habitat matrix is increasingly degraded. The dry forests and their associated floras and faunas are critically important to conserve, as their associated species have ecosystem impacts far beyond the dry forest habitats.

Mammals generally are believed to be much better known than other groups of animals, yet even the most basic question—How many species are there?—remains poorly answered. The discovery of mammal species new to science continues at an amazing rate, and in fact the rate of discovery has increased in recent years with the advent of modern systematic techniques. Some 25 to 30 species are now recognized as valid new species each year. A surprising number of these newly recognized species are primates and larger mammals (greater than 5 kilograms), groups that one might think are the best known. An analysis of recently described species suggests that the majority of newly recognized species are restricted to threatened areas of high endemism (Reeder et al. 2007).

The first level of research needed for SDTF mammals is modern systematic revisionary work to better understand species-level taxonomy and relationships of dry forest mammals. There are few preserved specimens of mammals from seasonally dry forests in the world's systematic collections, especially specimens that have preparations adequate for use with modern DNA

analyses; therefore, collections need to be augmented. Additionally, older specimens that are available need to be critically reevaluated. What is a species and which species occur in seasonally dry forests are basic questions that will provide the foundation for all future research and conservation efforts.

Compared with our knowledge of rain forest mammals, our knowledge of SDTF mammals is at a rudimentary state in terms of species diversity, ecology, and adaptations. Information about physiological adaptations of dry forest mammals comes predominantly from studies in desert environments that are extrapolated to closely related species occurring in dry forests or from studies of individual species. It will be critically important in future research to conduct comparative studies of mammalian clades among a gradient of habitats such as desert environments, SDTF, tropical moist forest, and tropical rain forest. Broad-scale comparative-type studies will help document the variation that exists in particular physiological and behavioral adaptations, and they will allow the distinction between those adaptations that are due to phylogenetic relationships and those that are true physiological and anatomical adaptations to particular environments. In particular, studies that focus on comparing one or only a few closely related species groups in different environments will be most useful in elucidating how important specific adaptations are for any one particular environment.

The study of the world's mammals is in an exciting phase of discovery, with new species still being described each year. Nevertheless, because of human development and land use throughout the tropics, and in seasonal forests in particular (Sánchez-Azofeifa et al. 2005, chap. 3), conservation issues faced by tropical mammals have never been more critical than the issues those species and environments face today. Although far more studies involving mammals in seasonally dry forests have been conducted in the Neotropics than in the Paleotropics, almost 80 percent of this research originated in only four countries—Mexico, Costa Rica, Brazil, and Panama. Although this may partially be explained by the distribution of seasonally dry forests (Miles et al. 2006), the mammalian faunas of several countries that contain dry forest, especially in Central America, have received little study. Future research should concentrate on including some of the lesser-studied regions that contain seasonally dry forests. Additionally, first-rate descriptive studies providing new information and critically evaluating previous studies will help clarify the role of mammals inhabiting seasonally dry forests. Well-documented, basic research is the foundation for science and the basis of intelligent conservation efforts.

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