American Journal of Primatology 72:104–112 (2010)

RESEARCH ARTICLE

The Effects of Extreme Seasonality of Climate and Day Length on the Activity Budget and Diet of Semi-Commensal Chacma Baboons (*Papio ursinus*) in the Cape Peninsula of South Africa

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We examined the effects of extreme seasonality on the activity budget and diet of wild chacma baboons with access to a high-quality, human-derived food source. The Cape Peninsula of South Africa is unusual among nonhuman primate habitats due to its seasonal extremes in day length and climate. Winter days are markedly shorter and colder than summer days but have higher rainfall and higher primary production of annually flowering plants. This combination of fewer daylight hours but higher rainfall is substantially different from the ecological constraints faced by both equatorial baboon populations and those living in temperate climates with summer rainfall. We sought to understand how these seasonal differences affect time budgets of food-enhanced troops in comparison to both other food-enhanced troops and wild foraging troops at similar latitudes. Our results revealed significant seasonal differences in activity budget and diet, a finding that contrasts with other baboon populations with access to high-return anthropogenic foods. Similar to nonprovisioned troops at similar latitudes, troop members spent more time feeding, socializing, and traveling during the long summer days compared to the short winter days, and proportionately more time feeding and less time resting in summer compared to winter. Summer diets consisted mainly of fynbos and nonindigenous foods, whereas winter diets were dominated by annually flowering plants (mainly grasses) and ostrich pellets raided from a nearby ostrich farm. In this case, food enhancement may have effectively exaggerated seasonal differences in activity budgets by providing access to a high-return food (ostrich pellets) that was spatially and temporally coincident with abundant winter fallback foods (grasses). The frequent use of both alien vegetation and high-return, human-derived foods highlights the dietary flexibility of baboons as a key element of their overall success in rapidly transforming environments such as the South African Cape Peninsula. Am. J. Primatol. 72:104–112, 2010.

Key words: seasonality; day length; food enhancement; raiding; commensalism; diet; activity budgets; foraging strategies

INTRODUCTION

Papio is one of the most successful and widespread primate genera, inhabiting a diverse range of habitats, climates and latitudes throughout sub-Saharan Africa. Adaptations that have facilitated baboons' success across such a wide range of habitats and extremes of seasonality include a highly omnivorous and flexible diet, a complex and variable social organization, a high degree of behavioral plasticity, flexibility and variability in mating systems, and both terrestrial and arboreal locomotor capabilities [Alberts & Altmann, 2006; Else, 1991; Henzi & Barrett, 2003; Whiten et al., 1987, 1991]. These traits have also allowed baboons to adapt easily to human altered environments [Else, 1991; Forthman Quick & Demment, 1988]. Baboons living in close proximity to human settlements typically modify their diets to include high-quality, human-derived foods, usually either agricultural products or human food waste (e.g., from garbage dumps) but also foods raided from homes, farms, or picnic sites [Altmann & Muruthi,

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Received 16 February 2009; revised 24 September 2009; revision accepted 24 September 2009

DOI 10.1002/ajp.20759

1988; Forthman Quick & Demment, 1988; Hill, 2000; Kansky & Gaynor, 2000].

Populations living on the urban fringe are largely ignored when it comes to testing socio-ecological theory. This is at least in part because regular raiding of high-quality, human-derived foods, available even when naturally occurring foods are scarce, can diminish seasonal effects and further complicate the already complex relationship between ecology and behavior [Altmann & Muruthi, 1988]. However, commensal populations of primates are becoming more prevalent and wildlife management is playing a growing role in the survival of wild primate populations. It is thus increasingly important to understand how a combination of anthropogenic and ecological pressures may together influence the behavioral ecology of wild primates.

The inclusion of high-quality foods from anthropogenic sources in the diet of primates has revealed that relatively low intake times can have significant effects on activity budgets [Altmann & Muruthi, 1988; Fa, 1991; Forthman Quick & Demment, 1988; Lee et al., 1986; O'Leary & Fa, 1993; Saj, 1999]. Compared with wild feeding troops, the feeding time of food-enhanced animals is significantly lower whereas time engaged in passive activities, such as resting, is significantly higher [Altmann & Muruthi, 1988; Brennan et al., 1985; Saj et al., 1999]. Traveling is either reduced, as has been observed in macaques [Schlotterhausen, 2000], or undertaken at a more leisurely pace, as shown for baboons [Altmann & Muruthi, 1988]. The effects of food enhancement on social time are unclear. Forthman Quick and Demment's [1988] study of raiding olive baboons (*Papio anubis*) is consistent with Dunbar's [1992] findings from wild foraging geladas in showing no obvious association between time spent feeding and time spent socializing. However, other studies of commensal baboons, vervets, and macaques have shown small increase in time spent socializing as a response to increased raiding behavior [Altmann & Muruthi, 1988; Brennan et al., 1985; Schlotterhausen, 2000]. Overall, commensalism appears to reduce time spent feeding and traveling, increase time spent resting, and minimize seasonal differences in behavior.

Current theory regarding the effects of season on the foraging strategies and activity budgets of primates focuses predominantly on wild foraging primates living in equatorial regions [Alberts et al., 2005; Bronikowski & Altmann, 1996; Dunbar, 1988, 1992; Foley, 1987; Post, 1981], where seasonal patterns differ considerably from temperate regions. Tropical regions experience little variation in day length and temperature, and seasons are generally defined as either wet or dry, as the amount of precipitation typically varies more than the average temperature. In contrast, temperate regions are more variable seasonally, with temperatures and day length lying at opposite extremes in winter vs. summer. As a result, baboons living in southerly latitudes face markedly different seasonal constraints compared with their equatorial counterparts. In most parts of southern Africa, for example, summers are wet and productive with considerably longer days and higher temperatures than winter. The South Western Cape region of South Africa, however, is characterized by a Mediterranean climate with hot, dry summers and cold, wet winters [Cowling et al., 1996]. Thus, in sharp contrast to most other temperate regions in Africa, annually flowering plant primary productivity is higher during the colder and shorter winter and spring days and lower during the hotter and longer days of summer and fall [Davidge, 1978b; Mucina & Rutherford, 2006]. The reduction in daylight hours during winter thus forces animals to compress their time budgets to meet their foraging requirements [Hill et al., 2003, 2004]. The higher winter productivity in the South Western Cape, however, might offset this constraint and mitigate the seasonal variation in time budgets that has been recorded in other studies within this region [e.g., Hill et al., 2003].

Variation in primate activity budgets during periods of low food availability may be explained theoretically in a number of ways. Schoener [1971], for example, proposed a useful theoretical framework within which to examine animal foraging strategies, focusing on a contrast between time-minimizing and energy-maximizing strategies. Time minimizers are predicted to spend as little time foraging as possible to meet their energetic needs. As food supplies increase, time minimizers should decrease their foraging effort as they meet their nutritional needs more easily. Geladas, macaques, and mangabeys have all been suggested to forage according to this model [Barton et al., 1992; Gaynor, 1994; Homewood, 1978; Iwamoto & Dunbar, 1983; Menard & Vallet, 1997]. Energy maximizers, on the other hand, would be expected to maintain a high level of foraging independent of food availability, a pattern that characterizes lemurs and vervet monkeys [Harrison, 1985; Vasey, 2005]. Some primates vary in the use of these strategies both among populations, e.g., orangutans [Rodman, 1977], and in accordance with local food availability, e.g., baboons [Gaynor, 1994] and macaques [Menard & Vallet, 1997]. It has also been suggested that baboons and macaques are essentially time minimizers but switch to a strategy of energy maximization during periods of food scarcity [Gaynor, 1994; Menard & Vallet, 1997].

Another response to a reduction in food availability during adverse conditions may lie with food selection. During periods of low food availability, primates may expand their diet to incorporate high-return foods [Alberts et al., 2005; Dunbar, 1983; Foley, 1987; Wrangham et al., 1998]. These high-quality foods often have increased exploitation costs but yield highly nutritious returns. This strategy is relatively atypical, but has been observed in geladas and chimpanzees, which supplement their diet with meat during periods of limited resources [Dunbar, 1983; Stanford et al., 1994; Stanford, 1996]. Human-derived foods usually fall into the category of high-return foods, and there is some evidence in baboons [Forthman Quick & Demment, 1988; Naughton-Treves et al., 1998] and macaques [Bell, 1984; Dittus, 1988; Pirta et al., 1997] that raiding of human settlements does increase when natural forage quality or quantity is low.

Alternatively, periods of low food availability may lead to an increased reliance on fallback foods. These are foods that are readily available in the environment but are nutritionally poor and typically result in an increase in total foraging time [Alberts et al., 2005; Altmann, 1998; Foley, 1987; Wrangham et al., 1998]. A switch to fallback foods during periods of low food availability has been reported for a number of species, including baboons [Alberts et al., 2005; Post, 1981], chimpanzees [Doran, 1997; Wrangham et al., 1991], langurs [Hladik, 1977], and vervets [Kavanagh, 1978]. Primates that increase their reliance on fallback foods are faced with the necessity of increasing foraging time at the expense of other, presumably less essential, activities.

In this study we aimed to assess the joint effects of (a) extreme seasonality in temperature and day length and (b) the availability of a high-quality, human-derived food resource on the activity budget and diet of a free-ranging troop of chacma baboons. We aimed to draw comparisons to both the nearby De Hoop population [which experiences similar seasonal extremes but without access to anthropogenic food sources; Hill, 1999; Hill et al., 2003] and an equatorial baboon population such as Amboseli [which experiences seasonality of rainfall, but not temperature or day length, and in which commensalism reduces the effects of seasonality on activity budgets; Altmann & Muruthi, 1988; Alberts et al., 2005]. In the Cape Peninsula, the combination of seasonal extremes, the presence of both high-return and fallback foods, and habitat diversity within the study troop's home range provided an opportunity to investigate whether semi-commensal chacma baboons are time minimizers or energy maximizers and whether they use fallback and/or high-return foods when natural food availability is low.

METHODS

Study Site

The study troop inhabits the South African Cape Peninsula, situated near the Southwestern-most tip of the African continent. This area falls within the greater Cape Town region and the baboon troops in this area are interspersed between several small and medium towns. The Peninsula forms part of the Cape Floristic Region, a global hotspot of biodiversity for higher plants and invertebrates [Cowling et al., 1996]. The predominant vegetation type of this area is fynbos, a distinctive shrub-like community of plants comprising the Proteacae, Ericaceae, and Restionaceae families. Soils are mostly nutrient-poor and the forage quality is thus low, resulting in relatively low numbers of endemic mammal species [Fraser, 1994]. In addition, alien plants such as *Pinus*, *Acacia* and *Eucalyptus* spp. have successfully invaded large tracts of the peninsula, with *Pinus* having been originally introduced by humans in plantations.

The Cape Peninsula has a Mediterranean climate and experiences considerable seasonal variation in temperature and rainfall. Winters are cool (7–20°C) and wet (monthly range 69–93 mm) with higher plant productivity whereas summers are warm (15–27°C) and dry [monthly range 15–17 mm; Cowling et al., 1996; South African Weather Service, 2009]. Although temperature and rainfall were not measured for this study, seasonal patterns during the study period were not unusual, nor were there any fires in the home range of the study troop that would have affected food availability. The Cape Peninsula receives winter rainfall and thus annually flowering plants (such as grasses belonging to the Poaceae family and *Trifolium* spp.) are predominantly available in winter [Milton, 2004] whereas fruit and flowers of fynbos plants are available year-round but most abundant in spring and summer [Johnson, 1992].

Study Troop—Plateau Road (PR)

The study troop, named Plateau Road (PR) after the road that transects its home range, is within 15 km of troops previously studied by Hall [1962a,b] and Davidge [1978a,b]. The PR troop inhabits an area with diverse land use practices that includes natural vegetation within the Cape of Good Hope section of the Table Mountain National Park, an ostrich farm, pine and eucalyptus plantations, alien invasive thickets of *Acacia* spp., approximately 12 houses, and a paved road running the length of the troop's home range where the baboons frequently encounter vehicles and are occasionally provisioned by people within these vehicles [van Doorn, 2009]. The troop consisted of 33 individuals, including 2 adult males and 14 adult females; 19 infants were born between April 2004 and September 2005, 12 of which survived to become juveniles. The high rate of infant mortality in this troop is consistent with that in other chacma baboons [e.g., Cheney et al., 2006] and likely related to high levels of infanticide as well as human-mediated mortality associated with commensalism.

Data Collection

Following a 4-month habituation period and interobserver reliability tests, data were collected by

A. van Doorn and 4 volunteer field assistants on individually identified adult troop members during all-day follows in summer (December 2004–February 2005) and winter (June–August 2005), totaling 59 observation days. We collected data from earliest to latest visibility (range: 06.00–19.30 hr) from an average distance of 5 m with no discernable effect on the behavior of the baboons. We typically located the troop at its sleeping site in the morning, and we stopped collecting data when the baboons returned to their sleeping site in the evening or if we lost sight of the troop for longer than 2 hr. We collected data evenly across the daylight hours in both seasons, from dawn to dusk, averaging 12.3 data collection hours in summer and 9.4 in winter; winter data collection hours were thus 23.6% shorter than summer data collection hours. Data collection hours were shorter than actual day length hours because there were periods during which we lost sight of the troop (e.g., when entering dense alien thickets). The occurrence of these periods did not vary between seasons, however, so the 23.6% difference between summer and winter data collection hours was close to the 27.8% actual difference in daylight hours across seasons [South African Weather Service, 2006].

We recorded instantaneous scan samples of habitat type and activity of all visible adult animals (individually identified) at 20 min intervals [Altmann, 1974], including details of food type when animals were engaged in feeding, using Handspring™ Visor handheld computers programmed with Pendragon® Forms software. Habitat types included fynbos (endemic vegetation comp of *Protea*, *Erica*, and *Restio* species), aliens (including trees: *Pinus* and *Eucalyptus* sp, thickets of *Acacia cyclops*, re-growth of previously cleared aliens, and grasses), alien & fynbos (a combination of both alien and fynbos species), ostrich pens (fenced pens covered with high grasses that were provisioned with ostrich pellets daily), and developed areas (including roads, buildings, houses, and offices). Behavioral categories included feed (actual ingestion of food), forage (preparation, handling, or manipulation of foodstuffs), search (slow movement while scanning the environment for food), raid (searching for and/or acquiring human-derived food), travel (nonsocial directional movement such as walking, running, or climbing), rest (nonsocial, inactive postures, such as sitting or lying down either alone or in contact with another individual), and social (aggressive and affiliative interactions, including grooming or being groomed by others). For the purpose of analyses, we combined the activities pertaining to the acquisition and manipulation of food (feed, forage, search, and raid) into a single feed category. We based our analyses on a total of 30 days in summer (267 hr, 761 scans) and 29 days in winter (202 hr, 603 scans).

Data Analysis

We converted data into hours [as in Hill et al., 2003, 2004] by organizing our scan samples into hourly time blocks. We then divided the number of times an activity was observed in that hour by the total number of scan records in that hour and multiplied by 60 to obtain minutes per hour. Monthly hours were then averaged to calculate the average number of hours individuals engaged in an activity per season [Hill et al., 2003, 2004]. This primary method of analysis was selected because percentage time budgets in southern populations experiencing substantial differences in day length would be calculated from different numbers of hours in each day and may not accurately reflect differences in activity allocation [Hill et al., 2003, 2004]. To evaluate whether each activity changed in proportion to day length, however, we also compared the percentage time budgets in the two seasons: a systematic increase or decrease across subjects would suggest a disproportionate change in time spent on that activity. We calculated activity budget proportions for each adult female by dividing the number of scans in which she engaged in a specific activity by the total number of scans for that female. We compared activity budgets between seasons using the Wilcoxon Matched Pairs Test. We calculated diet by tabulating the number of scan records during which each food type was consumed, converting this to a percentage of the total number of records. Finally, we determined the frequency of visits to the ostrich pens by calculating the number of scans during which the majority of the troop (>50%) was located within the ostrich pens.

Research reported here is original and adhered to the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates. Data were collected according to protocols approved by the University of Cape Town and South African National Parks, and adhered to the legal requirements of South Africa.

RESULTS

Activity Budget

PR baboons spent significantly more hours per day feeding (Wilcoxon Matched Pairs Test: $z = 3.351$, $P < 0.001$, $n = 16$), socializing ($z = 2.215$, $P < 0.05$, $n = 16$), and traveling ($z = 3.294$, $P < 0.001$, $n = 16$) in summer compared with winter (Fig. 1). There was no significant difference between seasons in hours per day spent resting (Wilcoxon Matched Pairs Test: $z = 1.022$, $P = 0.3$, $n = 16$). Neither feeding nor resting increased in simple proportion to the 23.6% increase (see above) in daylight hours: the percentage of time spent feeding was significantly higher in summer (median 41%, range 37–43%) than in winter (median 37%, range 29–55%; Wilcoxon Sign Rank Test: $z = 2.689$, $P = 0.007$, $N = 16$), or 45 min longer than would be

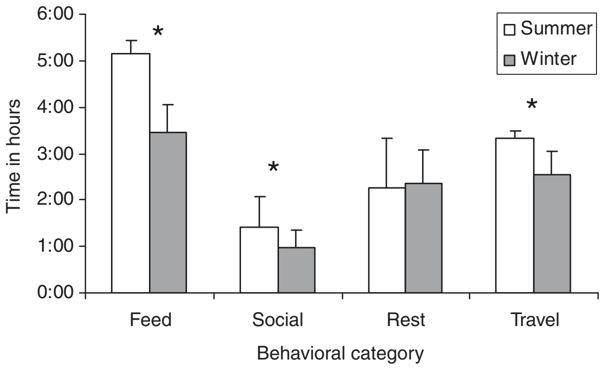

Fig. 1. Number of hours (median±interquartile range), calculated as per Hill et al. [2003, 2004], engaged in the four main activities (feed, social, rest, and travel; see text for definitions) in summer vs. winter. Significant differences ($P<0.05$) between seasons are denoted by an asterisk. Analyses were based on a total of 30 days in summer and 29 days in winter.

expected based on the increase in daylight hours. By contrast, the percentage of time spent resting was significantly lower in summer (median 16%, range 12–25%) compared with winter (median 23%, range 13–30%; Wilcoxon Sign Rank Test: $z=2.12$, $P=0.03$, $N=16$), or 22 min shorter than would be expected based on the increase in daylight hours.

A more detailed breakdown of foraging related activities revealed that the baboons spent significantly more time feeding on nonanthropogenic food sources and endemic vegetation in the summer than winter (Wilcoxon Matched Pairs Test: $z=3.52$, $P<0.001$, $n=16$; Fig. 2), and more time raiding in winter compared with summer (Wilcoxon Matched Pairs Test: $z=3.51$, $P<0.001$, $n=16$). In addition, the baboons spent proportionally more time searching for food ($z=3.36$, $P<0.001$, $n=16$) in winter than in summer (Fig. 3).

Diet

Analyses of the PR troop's diet also revealed significant seasonal differences (Fig. 4). Alien plants and fynbos were ingested significantly more often in summer than winter (Wilcoxon Matched Pairs Test, alien plants: $z=3.46$, $P<0.001$, $n=16$; fynbos: $z=3.52$, $P<0.001$, $n=16$). Conversely, the consumption of annuals and raided food was greater in winter than summer (Wilcoxon Matched Pairs Test: annuals: $z=3.52$, $P<0.001$, $n=16$; raided: $z=3.06$, $P<0.01$, $n=16$). Within the alien food category, PR had a significantly higher intake of acacia and pine seeds in summer compared with winter (Wilcoxon Matched Pairs Test: pines: $z=2.69$, $P<0.01$, $n=16$; seeds: $z=3.52$, $P<0.001$, $n=16$). In addition, underground storage items were eaten significantly more in winter than in summer (Wilcoxon Matched Pairs Test: $z=-2.227$, $P<0.05$, $n=16$). Analyses of frequency of visits to the ostrich pens also revealed significant differences between seasons, according to the hour of the day (Wilcoxon Matched Pairs Test: $z=-2.705$, $P<0.01$, $n=65$; Fig. 5).

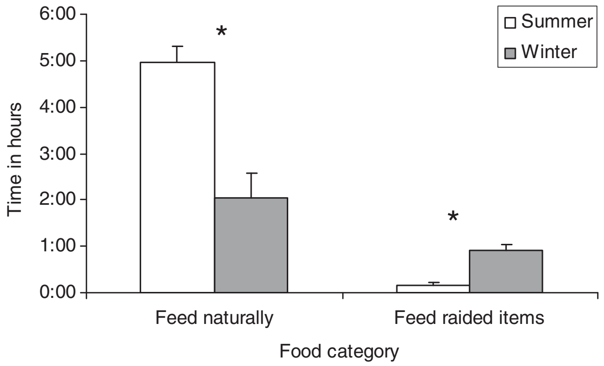

Fig. 2. Number of hours (median±interquartile range), calculated as per Hill et al. [2003, 2004], spent feeding on naturally occurring vegetation vs. raided items, such as ostrich pellets, in summer vs. winter.

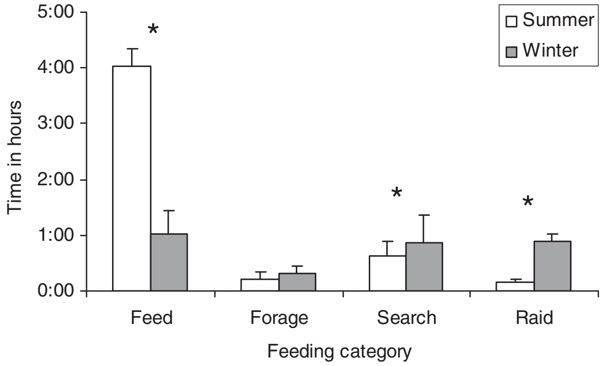

Fig. 3. Number of hours (median±interquartile range), calculated as per Hill et al. [2003, 2004], that adult females spent on foraging related behaviors (comprising the "feed" category in Fig. 1) in summer vs. winter. Significant differences between seasons ($P<0.05$) are denoted by an asterisk.

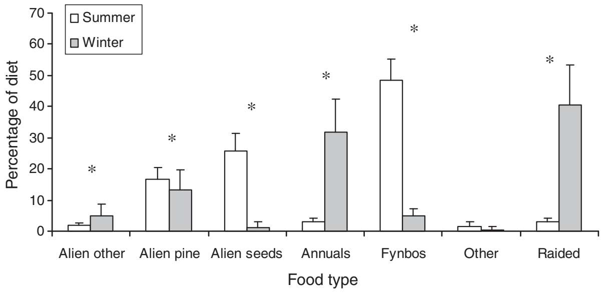

Fig. 4. Comparison of percentage of time, based on percentage of scan records, spent feeding on various food items in summer vs. winter. Significant differences ($P<0.05$) are denoted by an asterisk.

DISCUSSION

The activity budgets of the baboons in this study differed markedly between the seasonal extremes of

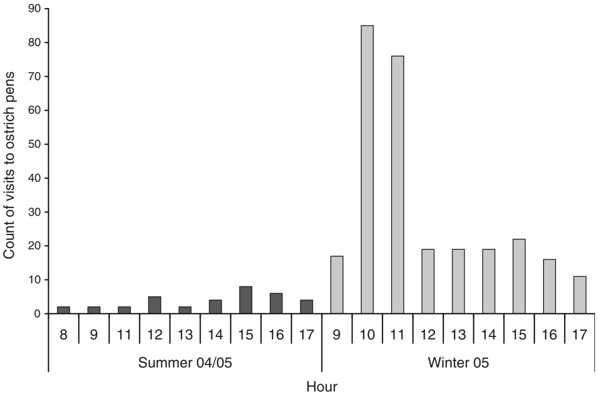

Fig. 5. Hourly breakdown of frequency of visits to the ostrich farm in summer vs. winter.

summer and winter, a departure from the reduced or absent seasonality of activity budgets found in other food-enhanced troops [Altmann & Muruthi, 1988; Bronikowski & Altmann, 1996; Eley et al., 1989]. The PR baboons spent significantly more time feeding, socializing, and traveling during the long summer days compared with the short winter days (Fig. 1). This pattern is similar to the nearby wild foraging De Hoop troops [Hill, 1999; Hill et al., 2003] that also increase the time they spend feeding, traveling, and socializing in the summer months. However, contrary to the De Hoop troops, which show a dramatic increase in resting time from winter to summer, there was no significant difference in resting time between the two seasons for the baboons observed in this study. The two studies also differ with regard to the magnitude of the increase in feeding time during the summer months. The De Hoop baboons only minimally increase their feeding time in summer compared with winter [less than an hour estimated from the figures in Hill et al., 2003], whereas the baboons in this study spent, on an average, 2.5 hr longer feeding during summer compared with winter. The seasonal differences in both feeding time and resting time in the PR baboons were not simply reflections of the difference in daylight hours; rather, feeding time was disproportionately higher and resting time was disproportionately lower in summer compared with winter.

The heightened seasonal differences in feeding time found in this study may differ from those of Hill [1999] and Hill et al. [2003] because at De Hoop, rainfall is more evenly distributed throughout the year, with more rainfall in early summer compared with the Cape Peninsula (e.g., approximately 38 mm in November and 24 mm in December vs. 8 and 13 mm, respectively, in the Cape Peninsula). This results in less clearly defined seasons at De Hoop and hence less variation in time spent feeding between summer and winter [Hill, 1999]. In addition, the PR troop was able to include more high-return, human-derived food items in their diet during the winter months, which may explain their markedly reduced feeding time during winter relative to summer. Baboons in De Hoop do not have similar access to anthropogenic food items during the winter months.

Seasonal differences in activity budgets are, in part, a reflection of differences in food availability across seasons, with increased foraging and/or traveling time typically associated with periods of lower food availability. This relationship is complicated in southern latitudes, however, by differences in daylight hours across seasons. The finding that the PR troop spends more time feeding, and feeds proportionally more, in summer would suggest that the summer, not the winter, is the season of relative food scarcity in the Cape Peninsula. This constraint may be offset by the increased daylight hours during this season, which may allow the baboons to increase their time spent foraging without compromising resting time (explaining the similar amount of resting time across seasons).

The dietary trends that emerged from this study, however, suggest that winter, not summer, may be the season of food scarcity for this population. In a metanalysis by Hill and Dunbar [2002], fruits and seeds emerged as foods preferred by baboons. The marked reduction of such foods (i.e., fynbos and alien seeds) in the diet of the PR baboons during winter suggests a possible shift in diet due to seasonal scarcity of preferred foods. Furthermore, the PR troop increased their reliance on subterranean food items in the winter season. These food items are energetically costly to excavate and are generally exploited when high-quality food is unavailable [Byrne et al., 1993; Hill & Dunbar, 2002; Whiten et al., 1987], suggesting again that winter may be the season of food scarcity.

Our findings are similar to those found by Davidge [1978a,b] in other wild foraging Cape Peninsula troops, which consumed the greatest amounts of fynbos in summer and increased their intake of grasses and annuals during winter, when fynbos is less productive [Johnson, 1992]. Preliminary qualitative analyses also suggest that in summer the baboons increased the diversity of their diet within the fynbos category, feeding selectively on fruits, flowers, and seed cones. While components of fynbos are reasonably rich in protein and energy, they require considerable processing time and are spatially dispersed. Increased day length in summer compared with winter would therefore allow the baboons more hours in which to forage and feed on diverse and spatially dispersed food items. This finding is supported by research in Amboseli [Post, 1982] showing that increased food availability leads to increased selection for diversity and in De Hoop where Hill [2006a] found that increased day lengths in the summer months led to greater dietary flexibility.

Lower feeding times in winter compared with summer may be largely explained by the significantly higher levels of ostrich pellet consumption by the PR troop during the winter months. This finding is consistent with studies of other semi-commensal baboons and macaques showing that raiding of anthropogenic food increases when natural food quality or quantity is low [baboons: Forthman Quick, 1986; Naughton-Treves et al., 1998; macaques: Bell, 1984; Dittus, 1988; Pirta et al., 1997]. Ostrich pellets may be categorized as a high-return food, as they are commercially-prepared to provide a high-calorie, nutrient-rich diet for ostriches and require minimal ingestion and handling time. As with other provisioned primates [Forthman Quick, 1986; Forthman Quick & Demment, 1988], the inclusion of an anthropogenic food source appears to have reduced required feeding time and the baboons were thus able to maintain a similar amount of time spent resting (Fig. 1) compared with summer despite the reduced daylight hours of winter.

The high-quality ostrich pellets comprised only a small component of the PR baboons' diet in the dry summer months. A closer look at the frequency of raiding the ostrich pens revealed that, despite visits to the ostrich farm at all hours in both seasons, the overall time spent at the farm was significantly higher in the winter months with a clear morning peak (Fig. 5). Ostrich pellets are available for only a brief period each day, as the ostriches consume the food when their feeding troughs are provisioned. The farmer deliberately varied feeding times to reduce the predictability and hence availability of this high-quality food item to the baboons. In winter months the troop would adopt a ''wait and see'' approach within the farm environs, whereas in summer the troop would visit the farm but seldom wait if there was no food available. This difference in approach to raiding may be explained by the abundance of grasses and flowering annuals in and around the farm during the wet winter months, providing the troop with ample fallback foods while they awaited a raiding opportunity. By contrast, in summer, grasses and annuals have senesced at the ostrich farm and with limited fallback foods a strategy that involves waiting for a high-return, temporally erratic food item may prove too costly. Moreover, high ambient temperatures and the absence of shade in and around the ostrich pens may have precluded the use of a ''wait and see'' approach during the summer months due to high thermoregulatory costs [Hill et al., 2006a,b]. These costs, in conjunction with the benefits of feeding on fynbos flowers, seeds, and fruits, may explain why the troop spends significantly less time at the farm and more time within the fynbos during the summer. This overall pattern, in which the baboons reduce their feeding time as they more easily meet their nutritional needs (via consumption of high-quality ostrich pellets), suggests that the PR troop uses a time minimizing rather than an energy maximizing foraging strategy [cf. Schoener, 1971].

The baboons in this study fed on a broad and variable set of foods, with percentage consumption varying seasonally for only a few of the major food items (e.g., fynbos, grasses, and annuals). These results suggest that this troop, like many other baboons, employs a ''hand off'' [Alberts et al., 2005] feeding strategy in which the baboons track and exploit a wide variety of foods varying in nutrient content, resulting in a highly variable diet across the year. The baboons in this study appear to rely on both ''fallback'' [Alberts et al., 2005; Altmann, 1998; Foley, 1987; Wrangham et al., 1998] and ''high-return'' [Alberts et al., 2005; Dunbar, 1983; Foley, 1987; Wrangham et al., 1998] foods when preferred foods are scarce, successively exploiting both low and high-quality foods as they become available. Similar patterns have been reported for other baboon populations across a diverse range of habitat types [Cape Peninsula: Davidge, 1978a,b; Hall, 1962a; Drakensberg: Byrne et al., 1993; Whiten et al., 1991; De Hoop: Gaynor, 1994; Hill et al., 2003]. These results, in conjunction with those of van Doorn [2009], which revealed marked seasonal shifts in home range use, suggest that Peninsula baboons are essentially dietary generalists [Alberts & Altmann, 2006; Hill & Dunbar, 2002; Norton et al., 1987], actively tracking a large number of different food types.

In conclusion, our results demonstrate strong seasonality in the activity budgets of the baboons in this study. This finding contrasts with the weak seasonality in activity budgets found for other semi-commensal baboon populations [Altmann & Muruthi, 1988], suggesting that the combination of a Mediterranean climate and seasonal differences in the use of high-return anthropogenic foods has resulted in a unique pattern of seasonal variation in Cape Peninsula baboon activity budgets. Short, wet winter days are characterized by the reduced availability of preferred natural food items (e.g., seeds and fruit) and an increase in the consumption of both abundant but low-quality fallback foods (e.g., grasses) and higher quality subterranean food items that are costly to excavate. The troop also responds to this period of relative food scarcity by increasing the amount of time they spend at the ostrich farm waiting for raiding opportunities. The cost of waiting for a temporally unpredictable high-return food source appears to be offset by abundant fallback foods (grasses and herbs) within the ostrich pens. Long, dry summer days, by contrast, are characterized by the consumption of a greater diversity of food items and a higher percentage of preferred dietary items (e.g., seeds and fruit). Together with a reduction in the consumption of both fallback foods and subterranean food items, our data suggest that summers in the Cape Peninsula are the periods of higher food availability but that these food items require more time to procure relative those consumed in winter and thus overall feeding time was significantly higher. The abundant use of both alien vegetation and high-return human-derived foods highlights the dietary flexibility of chacma baboons as a key element of their overall success at surviving in rapidly transforming environments such as the South African Cape Peninsula.

ACKNOWLEDGMENTS

We are grateful to South African National Parks for permission to conduct this research. We thank David Gaynor for his input in the initial project design and logistical support. Thanks to A. van Doorn's field assistants: Esme Beamish, Damiana Ravasi, Melissa Reisland, Nicholas Ellwanger, Joana da Silva, Catarina Rato, Tanya Rodriguez, Elizabeth Watts, and Chloe Burgan. Finally, we thank Marina Cords, Russell Hill, and one anonymous reviewer for their valuable comments and suggestions.

This manuscript reports original research that adhered to the American Society of Primatologists Principles for the Ethical Treatment of Non Human Primates. Furthermore, research was conducted according to protocols approved by the University of Cape Town and South African National Parks, and adhered to the legal requirements of South Africa.

REFERENCES

Alberts SC, Altmann J. 2006. The evolutionary past and the research future: environmental variation and life history flexibility in a primate lineage. In: Swedell L, Leigh SR, editors. Reproduction and fitness in baboons: behavioral, ecological, and life history perspectives. New York: Springer. p 277–303.

Alberts SC, Hollister-Smith JA, Mutata RS, Sayialel SN, Muruthi PM, Warutere JK, Altmann J. 2005. Seasonality and long-term change in a savannah environment. In: Van Schaik CP, Brockman D, editors. Seasonality in primates. United Kingdom: Cambridge University Press. p 157–196.

Altmann J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227–267.

Altmann J. 1980. Baboon mothers and infants. Cambridge: Cambridge University Press.

Altmann J, Muruthi P. 1988. Differences in daily life between semi provisioned and wild-feeding baboons. Am J Primatol 15:213–221.

Altmann S. 1998. Foraging for survival: yearling baboons in Africa. Chicago: University of Chicago Press. p 609.

Barton RA, Whiten A, Strum SC, Byrne RW, Simpson AJ. 1992. Habitat use and resource availability in baboons. Anim Behav 43:822–831.

Bell RHV. 1984. The man-animal interface: an assessment of crop damage and wildlife control. Conservation and wildlife management in Africa: the proceedings of a workshop organized by the U.S. Peace Corps at Kasungu National Park, Malawi.

Brennan EJ, Else JG, Altmann J. 1985. Ecology and behaviour of a pest primate: vervet monkeys in a tourist-lodge habitat. Afr J Ecol 23:35–44.

Bronikowski AM, Altmann J. 1996. Foraging in a variable environment: weather patterns and the behavioural ecology of baboons. Behav Ecol Sociobiol 39:11–25.

Byrne RW, Whiten A, Henzi SP, McCulloch FM. 1993. Nutritional constraints on mountain baboons (*Papio ursinus*): implications for baboon socioecology. Behav Ecol Sociobiol 33:233–246.

Cheney DL, Seyfarth RM, Fischer J, Beehner JC, Bergman TJ, Johnson SE, Kitchen DM, Palombit RA Rendall D, Silk JB. 2006. Reproduction, mortality, and female reproduction, mortality, and female reproductive success in chacma baboons in the Okavango Delta, Botswana. In: Swedell L, Leigh SR, editors. Reproduction and fitness in baboons: behavioral, ecological, and life history perspectives. New York: Springer. p 147–176.

Cowling RM, Macdonald IAW, Simmons MT. 1996. The Cape Peninsula, South Africa: physiographical, biological and historical background to an extraordinary hot-spot of biodiversity. Biodivers Conserv 5:527–550.

Davidge C. 1978a. Activity patterns of chacma baboons (*Papio ursinus*) at Cape Point. Zool Afr 13:143–155.

Davidge C. 1978b. Ecology of baboons (*Papio ursinus*) at Cape Point. Zool Afr 13:329–350.

Dittus WJP. 1988. Group fission among wild toque macaques as a consequence of female resource competition and environmental stress. Anim Behav 28:1249–1254.

Doran D. 1997. Influence of seasonality on activity patterns, feeding behaviour, ranging and grouping patterns of Täi chimpanzees. Int J Primatol 18:183–206.

Dunbar RIM. 1983. Theropithecines and hominids: contrasting solutions to the same ecological problem. J Hum Evol 12:647–658.

Dunbar RIM. 1988. Primate social systems. New York: Cornell University Press.

Dunbar RIM. 1992. Time: a hidden constraint on the behavioural ecology of baboons. Behav Ecol Sociobiol 31:35–49.

Eley RM, Strum SC, Muchem G, Reid GDF. 1989. Nutrition, body condition, activity patterns and parasitism of free ranging troops of olive baboons (*Papio anubis*) in Kenya. Am J Primatol 18:209–219.

Else JG. 1991. Nonhuman primates as pests. In: Box HO, editor. Primate responses to environmental change. London: Chapman and Hall. p 137–153.

Fa JE. 1991. Provisioning of Barbary macaques on the Rock of Gibraltar. In: Box HO, editor. Primate responses to environmental change. London: Chapman and Hall. p 137–153.

Foley R. 1987. Another unique species: patterns in human evolutionary ecology. New York: John Wiley and Sons.

Forthman Quick DL. 1986. Activity budgets and the consumption of human food in two troops of baboons, *Papio anubis*, at Gilgil, Kenya. In: Else J, Lee PC, editors. Primate ecology and conservation. Cambridge: Cambridge University Press. p 221–228.

Forthman Quick DL, Demment MW. 1988. Dynamics of exploitation: differential energetic adaptations of two troops of baboons to recent human contact. In: Fa JE, Southwick CH, editors. Ecology and behavior of food-enhanced primate groups. New York: Alan R Liss Inc. p 25–52.

Fraser M. 1994. Between two shores: flora and fauna of the Cape of Good Hope. South Africa: David Philip Publishers (Pty).

Gaynor D. 1994. Foraging and feeding behaviour of chacma baboons in a woodland habitat. PhD Dissertation, University of Natal, Durban, South Africa.

Hall KRL. 1962a. Numerical data, maintenance activities and locomotion of the wild chacma baboon, *Papio ursinus*. Symp Zool Soc Lond 139:181–220.

Hall KRL. 1962b. The sexual, agonistic and derived social behaviour patterns of the wild chacma baboon, *Papio ursinus*. Symp Zool Soc Lond 139:283–327.

Harrison MJS. 1985. Time budget of the green monkey, *Cercopithecus sabaeus*: some optimal strategies. Int J Primatol 6:351–376.

Hemingway CA, Bynum N. 2005. The influence of seasonality on primate diet and ranging. In: van Schaik CP, Brockman D, editors. Seasonality in primates: studies of living and extinct human and non-human primates. United Kingdom: Cambridge University Press. p 57–104.

Henzi P, Barrett L. 2003. Evolutionary ecology, sexual conflict, and behavioural differentiation among baboon populations. Evol Anthropol 12:217–229.

Henzi SP, Byrne RW, Whiten A. 1992. Patterns of movement by baboons in the Drakensburg mountains: primary responses to the environment. Int J Primatol 13:601–629.

Hill CM. 2000. A conflict of interest between people and baboons: crop raiding in Uganda. Int J Primatol 21:299–315.

Hill RA. 1999. Ecological and demographic determinants of time budgets in baboons: implications for cross-populational models of baboon sociobiology. PhD Thesis. University of Liverpool, UK.

Hill RA. 2006a. Thermal constraints on activity scheduling and habitat choice in baboons. Am J Phys Anthropol 129:242–249.

Hill RA. 2006b. Why be diurnal? Or, why not be cathemeral? Folia Primatol 77:72–86.

Hill RA, Dunbar RIM. 2002. Climatic determinants of diet and foraging behaviour in baboons. Evol Ecol 16:579–593.

Hill RA, Barrett L, Gaynor D, Weingrill T, Dixon P, Payne H, Henzi SP. 2003. Day length, latitude and behavioural (in) flexibility in baboons. Behav Ecol Sociobiol 53:186–278.

Hill RA, Barrett L, Gaynor D, Weingrill T, Dixon P, Payne H, Henzi SP. 2004. Day length variation and seasonal analysis of behaviour. S Afr J Wildl Res 34:39–44.

Hladik CM. 1977. A comparative study of the feeding strategies of two sympatric species of leaf monkeys: *Presbytis senex* and *Presbytis entellus*. In: Clutton-Brock TH, editor. Primate ecology. London: Academic Press. p 324–354.

Homewood KM. 1978. Feeding strategy of the Tana mangabey. J Zool Lond 186:375–391.

Iwamoto T, Dunbar RIM. 1983. Thermoregulation, habitat quality and the behavioural ecology of gelada baboons. J Anim Ecol 52:357–366.

Janson CH, Chapman CA. 1999. Resources and primate community structure. In: Fleagle JG, Janson CH, Reed KE, editors. Primate communities. Cambridge, UK: Cambridge University Press. p 237–267.

Johnson SD. 1992. Climatic and phylogenetic determinants of flowering seasonality in the Cape flora. J Ecol 81: 567–572.

Kansky R, Gaynor D. 2000. Baboon management strategy for the Cape Peninsula. Final report, Table Mountain fund project number ZA 568, Cape Town, South Africa. p 149.

Kavanagh M. 1978. The diet and feeding behaviour of *Cercopithecus aethiops tantalus*. Folia Primatol 30:30–63.

Kurup GU, Kumar A. 1993. Time budget and activity patterns of the lion-tailed macaque (*Macaca silenus*). Int J Primatol 14:27–39.

Lee PC, Brennan EJ, Else JG, Altmann J. 1986. Ecology and behavior of vervet monkeys in a tourist lodge habitat. In: Else JG, Lee PC, editors. Primate ecology and conservation. New York: Cambridge University Press. p 229–235.

Menard N, Vallet D. 1997. Behavioral responses of Barbary macaques (*Macaca sylvanus*) to variations in environmental conditions in Algeria. Am J Primatol 43:285–304.

Milton SJ. 2004. Grasses as invasive alien plants in South Africa. S Afr J Sci 100:69–75.

Mucina L, Rutherford MC. 2006. The vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19. Pretoria: South African National Biodiversity Institute. p 807.

Naughton-Treves L, Treves A, Chapman C, Wrangham R. 1998. Temporal patterns of crop-raiding by primates: linking food availability in croplands and adjacent forest. J Appl Ecol 35:596–606.

Norton GW, Rhine RJ, Wynn GW, Wynn RD. 1987. Baboon diet: a five-year study of stability and variability in the plant feeding and habitat of the yellow baboons (*Papio cynocephalus*) of Mikumi National Park, Tanzania. Folia Primatol 48:78–120.

O'Leary H, Fa J. 1993. Effects of tourists on Barbary macaques at Gibraltar. Folia Primatol 61:77–91.

Pirta RS, Gadgil M, Kharshikar AV. 1997. Management of the rhesus monkey *Macaca mulatta* and Hanuman langur *Presbytis entellus* in Himachal Pradesh, India. Biol Conserv 79:97–106.

Post DG. 1978. Feeding and ranging behavior of yellow baboon (*Papio cynocephalus)* in the Amboseli National Park, Kenya. PhD Dissertation, Yale University, New Haven.

Post DG. 1981. Activity patterns of yellow baboons (*Papio cynocephalus*) in the Amboseli National Park, Kenya. Anim Behav 29:357–374.

Post DG. 1982. Feeding behaviour of yellow baboons (*Papio cynocephalus*) in the Amboseli National Park, Kenya. Int J Primatol 3:403–430.

Rodman PS. 1977. Feeding behaviour of orangutans of the Kutai Nature reserve, East Kalimatan. In: Clutton-Brock TH, editor. Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys and apes. London: Academic Press. p 383–413.

Saj T. 1999. The ecology and behaviour of vervet monkeys in a human modified environment (*Cercopithecus aethiops*). MSc Thesis, University of Calgary, Calgary, Canada. Dissertation Abstracts International.

Saj T, Sicotte P, Paterson JD. 1999. Influence of human food consumption on the time budget of vervets. Int J Primatol 20:977–994.

Schlotterhausen L. 2000. Town monkeys, country monkeys: a socioecological comparison of a human commensal and wild group of bonnet macaques (*Macaca radiata*). PhD Dissertation, New York University, New York, NY.

Schoener TW. 1971. Theory of feeding strategies. Ann Rev Ecol Syst 2:369–404.

South African Weather Service. 2006. Data for station 0004891 9: Cape Point latitude: 34.3530 longitude: 18.4890 244 m 2003–2005.

South African Weather Service. 2009. http://www.weathersa.co.za/Climat/Climstats/CapeTownStats.jsp.

Southwick CH. 1967. An experimental study of intragroup agonistic behavior in rhesus monkeys (*Macaca mulatta*). Behaviour 28:182–209.

Stanford CB. 1996. The hunting ecology of wild chimpanzees: implications for the evolutionary ecology of Pliocene hominids. Am Anthropol 98:96–113.

Stanford CB, Wallis J, Mpongo E, Goodall J. 1994. Hunting decisions in wild chimpanzees. Behaviour 131:1–18.

Vasey N. 2005. Activity budgets and activity rhythms in red ruffed lemurs (*Varecia rubra*) on the Masoala Peninsula, Madagascar: seasonality and reproductive energetics. Am J Primatol 66:23–44.

van Doorn A. 2009. The interface between socioecology and management of chacma baboons (*Papio ursinus*) in the Cape Peninsula, South Africa. PhD Dissertation. University of Cape Town, Cape Town, South Africa.

Whiten A, Byrne RW, Henzi SP. 1987. The behavioural ecology of mountain baboons. Int J Primatol 8:367–388.

Whiten A, Bryne RW, Barton RA, Waterman PG, Henzi SP. 1991. Dietary and foraging strategies of baboons. Phil Trans Royal Soc Lond B 334:187–197.

Wrangham RW, Conklin NL, Chapman CA, Hunt KD. 1991. The significance of fibrous foods for Kibale Forest chimpanzees. Phil Trans R Soc Lond B 334:171–178.

Wrangham RW, Conklin-Brittain NL, Hunt KD. 1998. Dietary responses of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I Antifeedants. Int J Primatol 19:949–970.