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RESEARCH ARTICLE

Differential Effects of Unusual Climatic Stress on Capuchin (*Cebus capucinus*) and Howler Monkey (*Alouatta palliata*) Populations on Barro Colorado Island, Panama

KATHARINE MILTON[1]* AND JACALYN GIACALONE[2]
[1]*Department Environmental Science, Policy and Management, University of California, Berkeley, California*
[2]*College of Science and Mathematics, Montclair State University, Montclair, New Jersey*

Though the harmful effects anthropogenic disturbances pose to wild primates are well appreciated, comparatively little is known about the effects of natural disturbances. From December 2010 to January 2011, different mortality patterns were observed for two primate species, capuchins and howler monkeys, on Barro Colorado Island (BCI), Panama. Unusually high rainfall in 2010 was associated with census and cadaver data indicating the rapid loss of >70% of the capuchin population in late 2010 to early 2011. In contrast, over this same period, no decline was documented for howler monkeys and cadaver data for howlers was unexceptional. The high mortality experienced by the capuchin population was unexpected and its extent was not fully appreciated until the event was largely over. Explanations proposed for it included effects of hypothermia, disease or a shortage of some essential nutrient(s). Of these, the dietary explanation seems most probable. BCI capuchins depend most heavily on arthropod foods in December, when few higher quality ripe fruits are available. The unprecedented high rainfall in December 2010 is hypothesized to have largely eliminated the arthropod peak expected on BCI each December. A lack of protein-rich arthropods, when coupled with the climatic and nutritional stress capuchins generally experience at this time of year, appears to have precipitated the rapid die-off of most of the island's capuchin population. As howler monkeys obtain dietary protein primarily from leaves, a shortage of edible arthropods would not affect howler numbers. Comparison of our 2010 data with similar data on earlier primate/mammalian mortality events reported for BCI and for Corcovado, Costa Rica indicates that our understanding of the effects of natural disturbances on wild primate populations is not profound. We suggest that more research be devoted to this increasingly timely topic, so important to conservation policy. Am. J. Primatol. © 2013 Wiley Periodicals, Inc.

Key words: Cebidae; mortality; natural disturbances; rainfall; protein deficiency; arthropods

INTRODUCTION

Some 50% of wild primates are currently threatened by anthropogenic disturbances such as habitat loss and hunting [Bracebridge et al., 2012; Lambert, 2011]. Although the negative effects of human-induced disturbances are well appreciated [Chapman et al., 2000; Johns & Skorupa, 1987; Phoonjampa et al., 2011; Remis & Robinson, 2012], those posed by *natural* disturbances are less well studied or understood. Because natural disturbances can negatively affect primates and other fauna in even well protected environments, it is important to better understand their short- and long-term effects on primate population parameters and sustainability [Ramirez-Barajas et al., 2012; Wiederholt & Post, 2010]. This is particularly true today as global warming appears to be altering climatic features in ways detrimental to wild primates. To evaluate the potential impact of natural disturbances, relevant data are needed on parameters of affected wild populations and characteristics of their habitat both prior to and following the natural disturbance. Because such data are often not available, it can be

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*Correspondence to: Katharine Milton, Department Environmental Science, Policy and Management, 130 Mulford Hall, University of California Berkeley, CA 94720-3114. E-mail: kmilton@berkeley.edu

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difficult to determine what effects a natural disturbance has in fact produced. In spite of this difficulty, there are some published data on this topic. For example, Li et al. [2009] reported a decrease of ~27% in the average group size of Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) following unusually heavy snowstorms in China in 2008, while Pavelka et al. [2007] described an 88% decline in population size for Belizean black howler monkeys (*Alouatta pigra*) following Hurricane Iris. Similar accounts describe effects of severe tropical storms [Balki & Underwood, 2005; Dittus, 1985; Tsuji & Takatsuki, 2008], prolonged drought [Gould et al., 1999; Hamilton, 1985], or drought and fire [Berenstain, 1986].

Natural disturbances can change group structure and mating opportunities by altering the sex ratio of adults and reduce population growth if adult females or immature monkeys experience high rates of mortality or periods of subfertility [Li et al., 2009]. The rapid loss of a high percentage of a population can affect its genetic diversity and future viability [Milton & Hopkins, 2006]. Below we present data on another type of natural disturbance, namely unusually heavy rainfall, and the associated changes noted in the population parameters of two primate species, capuchin monkeys (*Cebus capucinus*) and howler monkeys (*Alouatta palliata*) on Barro Colorado Island (BCI), Panama. Between mid-December 2010 and late January 2011, the capuchin population suffered high mortality while the howler population did not. We use our census and mortality data in combination with climatic and other data available for BCI to evaluate several explanations advanced to explain the high capuchin mortality and then compare our results with those reported for earlier primate/mammalian mortality events for BCI and Corcovado, Costa Rica.

METHODS

This study was non-invasive. All work was conducted in compliance with national and institutional regulations and adhered to the legal requirements of the Republic of Panama and ASP principles for the ethical treatment of nonhuman primates.

Study Site

BCI (9°10′N, 79°51′W), a 1,500-ha island in Lake Gatun, Panama, was formed in 1914 after the Chagres River was dammed to create a water supply for the Panama Canal. Today, the entire island is covered in tropical moist forest [Holdridge & Budowski, 1956], with many areas estimated to be >300 years old [Hubbell & Foster, 1990]. In 1923, BCI was declared a nature reserve and has since served as the site for numerous and varied scientific field studies. Extensive data have been compiled on many physical features of the island and on its climate, flora, and fauna [e.g., Leigh et al., 1982]. These include almost a century of data on rainfall, temperature and other climatic features as well as extensive data on phenological production patterns of the island's tree species, annual patterns of arthropod abundance, the diet and population parameters of the island's resident primate species and annual mortality pattern of BCI mammals. Such baseline data can assume critical importance when a natural disturbance occurs, for they can provide the information required to critically evaluate the impact of such events on particular primate or other taxa and help identify the factors implicated in any associated changes. Indeed, it is only because there were baseline data for BCI on the two primate populations and on many key environmental parameters, that it was possible for us to report these findings.

Rainfall Data

In 1929, the Panama Canal Administration began collection of daily rainfall data on BCI, a practice continued until the present day. These data were augmented in 1971 by a weather station established by the Smithsonian Tropical Research Institute (STRI), which manages BCI [Smythe, 1982]. BCI receives an annual average of 2,649 ± 476 mm of rainfall (1929–2011) though there is considerable interannual fluctuation (Fig. 1). The annual rainfall pattern divides the year into two seasons: an approximately 4-month dry season January–April and a wet season lasting May into December (Fig. 2). On average, October and November are the 2 wettest months. Mid-December generally marks the end of the rainy season and transition into the dry season. Though temperature shows little annual variation, the 2 wettest months, October and November, also show lowest mean annual temperatures [Richards & Windsor, 2007].

Primary Productivity

A number of studies have examined primary productivity on BCI [Foster, 1982a,b; Milton, 1980; Milton et al., 2005; Smythe, 1982; Wolda, 1982; Wright et al., 1999]. Ripe fruit production generally peaks in February and then declines over the rest of the year [Milton et al., 2005]. In the late rainy season, extending though December, few species of ripe fruit are available either per hectare or on the island as a whole and, as a consequence, this period is a time of hunger stress for many animals [Foster, 1982a,b; Milton, 1980; Milton et al., 2005; Smythe et al., 1982; Wright et al., 1999]. Young leaves peak in abundance during the early wet season May–June and are least abundant in the late rainy and early dry seasons [Leigh & Windsor, 1982; Milton, 1980; Wolda, 1982; Wolda & Foster, 1978].

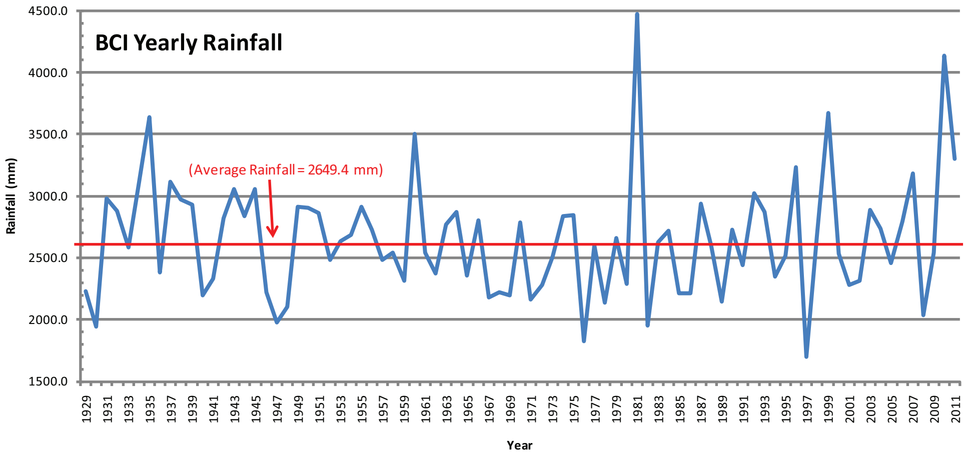

Fig. 1. Yearly rainfall in millimeters for Barro Colorado Island, Panama, 1929–2011. Overall average = 2,649 mm (Steve Paton, Physical Monitoring Program, STRI).

Arthropod Abundance

A number of studies have estimated arthropod abundances on BCI. Depending on the study, weekly, monthly, seasonal, and annual arthropod abundance has been examined in leaf litter, in the understory, in light gaps and at various levels in the forest canopy [Gradwohl & Greenberg, 1982; Levings & Windsor, 1982; Richards & Windsor, 2007; Smythe, 1974, 1982; Stunz et al., 2003; Wolda, 1982; Worthington, 1982]. All types and size classes of BCI arthropods show some evidence of seasonal and interannual fluctuations [Smythe, 1974, 1982; Wolda, 1982, 1992]. A very strong predictable major peak in arthropod numbers typically occurs at the beginning of the rainy season each year in May–June, followed by a smaller but still predictable second peak in arthropod numbers in December–January, this latter peak largely due to the migration of Coleoptera and a minor emergence of Hymenoptera [Smythe, 1982]. The December–January arthropod peak, as discussed below, appears to be of critical dietary importance to BCI capuchins [Oppenheimer, 1982].

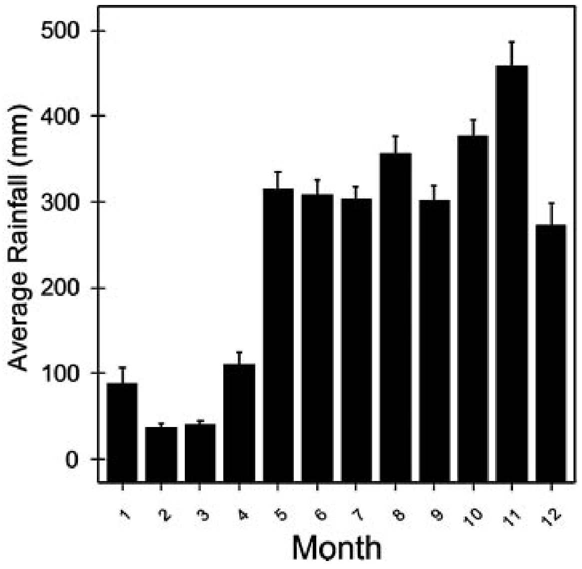

Fig. 2. Average monthly rainfall in millimeters for Barro Colorado Island, Panama, 1929–2011 (Steve Paton, Physical Monitoring Program, STRI).

BCI Primate Species

Free-ranging populations of howler, capuchin and tamarin (*Saguinus geoffroyi*) monkeys were already present in forests on what became BCI prior to formation of the island, and their descendants occur there today. Howler monkeys (adult body mass = 7–9 kg) are by far the most abundant BCI primate, with an estimated population size in March 2010 of ~1,200 monkeys, distributed more or less uniformly over the island in 60–70 groups [Milton, 1982, 1996; Milton et al., 2005; Milton, unpublished data]. Both howler population size and the total number of howler groups on BCI have remained relatively constant since the late 1960s [Milton, 1982, 1996; Milton et al., 2005]. Capuchins (adult body mass = 2.7–3.8 kg) are the second most abundant BCI primate, with an estimated population size in March 2010 of ~300 monkeys, distributed more or less uniformly over the island in some 15–18 groups (J.G., unpublished data). Prior to late 2010, capuchin population size and the number of groups on the island had remained relatively constant since at least the mid-1960s [Milton et al., 2005; Mitchell, 1989; Oppenheimer, 1982]. The third primate species on BCI, red-naped tamarins (adult body mass = 500 g), occurs on the island in low numbers ($\leq$50 individuals total). Black-handed spider monkeys (adult body mass = 7–9 kg) had been extirpated from the area by hunters prior to the formation of BCI. In the late 1950s, a small number of young spider monkeys were introduced onto BCI and provisioned until they could forage independently [Milton, 1981]. By 2005, the BCI spider monkey population had gradually increased to a size of ~25 individuals [Milton & Hopkins, 2006], living in a single social group. Night monkeys (*Aotus lemurinus*) are native to this region of Panama but their presence on BCI today is uncertain.

Annual Pattern of Mammal Mortality

On BCI, mammal mortality, including primate mortality, is generally low during the dryer half of the year [Milton, 1982, 1990, 1996; Milton et al., 2005; Wright et al., 1999]. After the rains begin in May, mortality begins to rise, typically reaching its peak in the late rainy season [Foster, 1982b; Milton, 1990]. The annual peak in mammal mortality is hypothesized to relate primarily to dietary stress induced by the island-wide decline in higher quality plant foods, particularly ripe fruits [Foster, 1982b; Milton, 1982, 1990, 1996; Milton et al., 2005; Wright et al., 1999]. The cool wet conditions and lower temperature at this time of year may also contribute to the late rainy season mortality peak.

Dietary Behavior of Howlers and Capuchins

During most of the year, howler monkeys on BCI eat a mixed diet composed primarily of ripe fruits and young leaves [Milton, 1980]. In the late rainy season, however, when few canopy species are producing ripe fruits, howler monkeys turn heavily to young leaves as a dietary staple and can live on diets composed largely of leaves for weeks [Milton, 1980]. Many species of young leaves and some mature leaves provide howlers with high quality protein [Hladik, 1978; Milton, 1979, 1980]; howlers are also estimated to obtain $\geq$33% of their required daily energy from fatty acids produced in fermentation of dietary fiber [Milton & McBee, 1983]. These sources of protein and energy, along with any stored body fat and available fruits, generally carry most howler monkeys through the late rainy season each year and into the dry season when dietary and climatic conditions improve.

The late rainy season dietary behavior of BCI capuchins differs notably from that of howlers. For most of the year, ripe fruits from large canopy tree species dominate the diet of capuchins, making up 85–90% of their daily feeding periods [Oppenheimer, 1982]. Fruits are supplemented with animal source foods (generally ~10–15% of daily feeding periods), primarily arthropods but occasionally eggs, nestlings, or small mammals [Oppenheimer, 1982; see also Mitchell, 1989]. Cluster analysis shows, however, that from late September to mid-December, capuchins on BCI largely abandon foraging for fruits in canopy trees, instead foraging primarily for smaller fruits from a few short, small-crowned understory tree species [Mitchell, 1989]. Such understory fruits, though generally abundant at this time of year [Foster, 1982a; Mitchell, 1989], are speculated to be lower in quality than the larger sized fruits capuchins preferentially feed on most of the year [Mitchell, 1989]. Arthropods, of daily importance in the capuchin diet, increase in importance in the late rainy season [Mitchell, 1989; Oppenheimer, 1982], apparently to compensate for the decline in fruit quality [Mitchell, 1989]. In December, the contribution of arthropods to the capuchin diet reaches its annual peak when these monkeys spend an average of 40% of their daily feeding periods actively consuming arthropod prey [Oppenheimer, 1982].

Unlike excess dietary energy, which can be stored as body fat and used in times of need, protein as such cannot be stored by the mammalian body except in minute amounts and must therefore be consumed in foods each day [Maynard et al., 1979]. Thus to remain in positive nitrogen balance, it is essential for capuchins to have an adequate supply of arthropods or other viable protein sources available to them throughout the year. Most ripe fruits, though containing some protein, are not regarded as sufficient to meet capuchin protein requirements. If fruits did provide sufficient protein, we assume BCI capuchins would not spend a high percentage of their foraging time each day throughout the year specifically seeking out arthropods and other animal source foods [Mitchell, 1989; Oppenheimer, 1982].

Primate Mortality Data

Since 1986, K.M. has managed a program to collect and curate the skulls of all monkeys found dead in the BCI forest. Many people carrying out fieldwork occasionally encounter primate remains. K.M. offers a financial reward for each primate skull turned in to her collection. Data sheets record the date, place, name of the finder, and condition of the cadaver. In the 26 years of the collection's existence, >480 primate skulls have been recovered. The majority are those of howler monkeys but all four primate species are represented in the collection. The annual pattern of primate mortality on BCI, as evidenced from skull collection data, accords with the mortality pattern exhibited by the mammal community as a whole, with the mid-to-late rainy season August–November showing highest mortality [see Milton, 1982, 1990, 1996].

Census Data

At approximately the same time each year, generally January–February, J.G. and Greg Willis come to BCI to carry out a mammal survey. Using a strip-census sampling technique [Glanz, 1982], over a period of several weeks, they walk the trails on BCI from 6:45 a.m. until noon, moving at a rate of 1 km/hr.

The census continues virtually every day until >100 km of trail have been covered. Each time mammals are seen, the location, species, and number of individuals are recorded. Monkey sightings (all species) are routinely recorded along with sightings of other mammals. Once the census is completed for that year, the total number of individuals of each species recorded is then divided by the number of kilometers covered in that census to calculate an index of sightings as well as density estimates by King's method [Glanz, 1982]. This mammal census was begun in 1986 with the most recent census completed in 2012.

RESULTS

2010 Rainfall

In 2010, total rainfall recorded for BCI was 4,135 mm, >1,500 mm higher than the annual average for BCI (Fig. 3), and the second wettest year on record. When rainfall for each month of 2010 is compared with average rainfall for that month (1929–2011), 10 months of 2010 showed higher than average rainfall; beginning in June 2010, rainfall was higher than average for 7 consecutive months (Fig. 4). Typically, December is characterized by a sharp drop in rainfall and marks the transition into the dry season (Figs. 2 and 4). Average rainfall for December is estimated at 240 mm. In December 2010, rainfall approached 1,200 mm, almost five times the monthly average, and the highest December rainfall ever recorded for BCI (Fig. 4).

Rain fell on >50% of the days in December 2010, often for prolonged periods. In the first 3 days of December, cumulative rainfall was higher than the total monthly average for December. This was followed by considerably more rain December 6 through December 9. The total amount of rain reported for the first 9 days of December 2010 approached three times the monthly average for December. Heavy rainfall was also recorded on other days in December and rain continued to fall through the first week of January 2011.

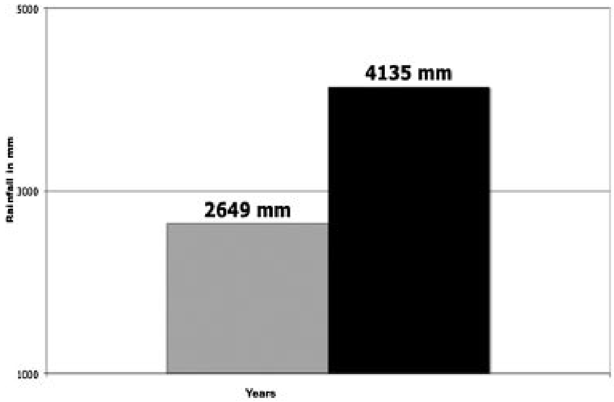

Fig. 3. Barro Colorado Island, 83-year average for annual rainfall versus total rainfall for 2010. Gray bar on left represents the 83-year average (2,649 mm); black bar on right shows total rainfall for 2010 (4,135 mm).

Capuchin and Howler Mortality

Before December 9, 2010 only three primate skulls (one howler monkey and two capuchins) had been turned in to K.M.'s skull collection that year. Between November 14 and December 9, 2010, though walking in the forest almost every day for hours, K.M. did not find any dead monkeys or encounter the remains of other dead mammals nor were any primate skulls turned in to her collection. Thus, prior to mid-December 2010, primate and island-wide mammal mortality appeared low.

For primates, this picture changed after the heavy rainfall in early December. On December 9, the cadaver of an infant howler was found and on December 13, two capuchin and one howler cadavers were found. From that point, continuing into early February 2011, primate remains were relatively common. Between December 9, 2010 and February 8, 2011, 27 primate skulls were turned in to K.M.'s collection: 14 howler monkeys, 12 capuchins, and 1 tamarin. Eleven of the 27 dead primates were found between December 9 and December 31, 2010. Typically, December cadavers were described as "fresh," "intact," or "whole"—descriptive terms indicating the monkey had died very recently. Some primate remains discovered in January 2011 were also described as "fresh" or "whole" but others were described as "whole skeleton" or "only bones"—descriptive terms indicating these monkeys had likely died at an earlier date. After February 8, 2011, no more monkey remains of any species were turned in to the collection until after the rains started again in April.

Howlers occur on BCI at a ratio of approximately 4:1 relative to capuchins but the number of monkey cadavers found over this 2-month period was nearly equal for the two species. Assuming cadavers of both species have an equal probability of being discovered, finding a similar number of cadavers of both species over this short period suggests mortality was proportionately higher for capuchins. K.M.'s primate mortality data show that it is not unusual for as many as 20 to >30 howler cadavers to be found per year on BCI. For example, in the years 1990, 1996, and 2000, the numbers of howler cadavers recovered were 23, 22, and 36, respectively. In contrast, the number of capuchin cadavers turned in to the collection per year typically ranges from none to two. Given the far larger population size of howler monkeys, finding 14 dead howlers over a 2-month period is not unusual whereas finding 12 dead capuchins over the same period is unprecedented and indicates high capuchin mortality.

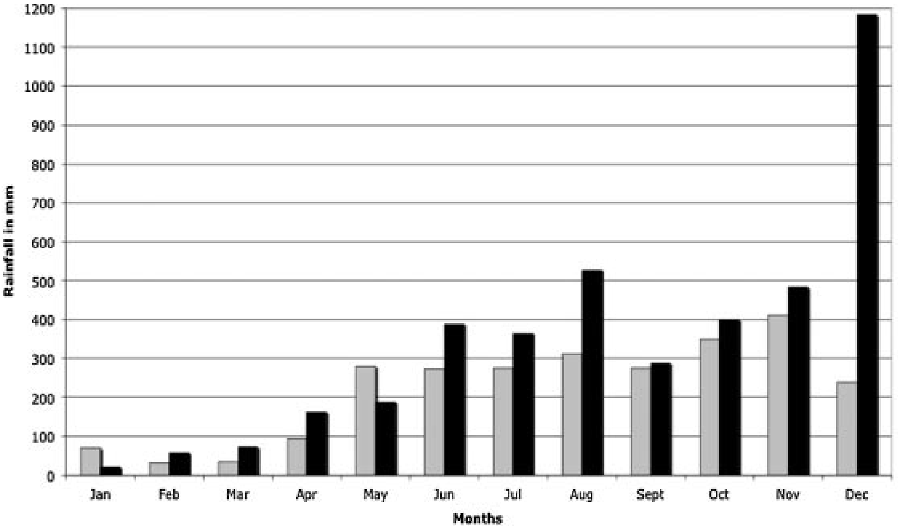

Fig. 4. Barro Colorado Island, Panama, 83-year average in millimeters for monthly rainfall versus monthly rainfall for 2010. Gray bars represent average monthly rainfall while black bars indicate monthly rainfall for 2010.

Age estimates derived from the dentition of the capuchin and howler monkey skulls turned in to the collection between December 9, 2010 and February 8, 2011 indicate different mortality patterns for the two populations. All 12 capuchin cadavers appeared to be those of old juvenile and sub-adult animals (age categories of Di Bitetti and Janson [2000]; mean = 3.7 ± 1.1 years ($N = 12$ skulls). In contrast, the estimated mean age for the 14 howler cadavers was bimodal with animals either extremely old (mean = 23.1 ± 2.9 years; $N = 8$) or very young (mean = 0.67 ± 0.43 years; $N = 6$). Thus in the capuchin population, the late juvenile and sub-adult classes were most heavily impacted while for howlers it was the very old and very young.

Capuchin and Howler Monkey Census Results

Census data support our interpretation of high capuchin mortality. Data compiled by J.G. for capuchin monkey sightings over the 26-year period 1986–2012 are presented in Figure 5A. These data make clear that in 2011 and 2012, population estimates for BCI capuchins were extremely low. Twenty-six years (1986–2012) of census data show an overall average of 1.0 capuchin sighted per kilometer of trail censused. In January–February 2010, this figure was 1.0, but by February 2011, it had declined to 0.28 capuchin sightings per kilometer of trail and by February 2012, to 0.23 sightings per kilometer. Following the 2010 die-off event, no capuchin infants (infant = 0–12 months of age) were observed in the BCI forest until January 2012. Such census results indicate that ~72% of the capuchin population died between mid-December 2010 to early February 2011. King's estimator [see Glanz, 1982 for methodology] based on the strip-census data indicates a total capuchin population decline of 77% between March 2010 and February 2011. In contrast, J. G.'s strip census data for howler monkeys over the same period show a slight increase in howler numbers (Fig. 5B). Census data for BCI howler monkeys compiled each year from 1977 through 2012 by K.M. [see Milton, 1996; Milton et al., 2005 for protocols] independently confirm that the howler population suffered no detectible decline in size over this period.

DISCUSSION

Our data indicate that an estimated 72–77% of the BCI capuchin population died within a few weeks in late 2010 to early 2011, while the island's howler monkey population was not similarly affected. Of the various explanations considered to account for the differential mortality between the two populations (i.e., hypothermia, disease, dietary shortage), we consider an acute shortage of dietary protein the most probable explanation for the high capuchin mortality—this lack of protein hypothesized to relate to the negative effects of prolonged heavy rainfall on the expected arthropod peak in December 2010. In contrast, as howler monkeys obtain dietary protein primarily from young leaves, a low supply of arthropods in late 2010 would not affect howler numbers. If disease were involved in the high capuchin mortality, we assume such disease would affect capuchins of all ages as well as other monkey species on BCI. Though no autopsies were performed to rule out disease, we believe the possibility of a disease outbreak is unlikely (see also below for information on a primate mortality event in Costa Rica where autopsies were performed and no

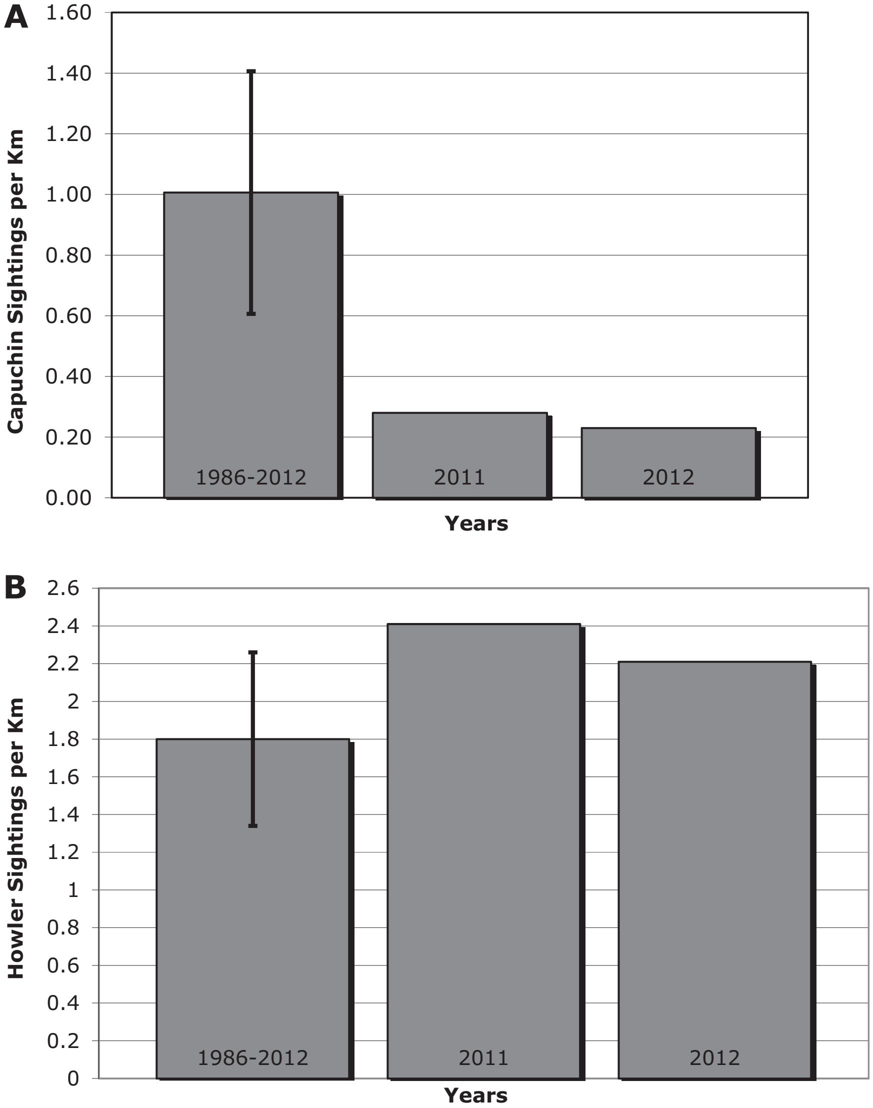

Fig. 5. (A) Mean (±1 SD) number of individual capuchins sighted per kilometer walked in combined data for years 1986–2012 versus number of individual capuchins sighted per kilometer walked for 2011 and 2012, Barro Colorado Island, Panama. (B) Mean (±1 SD) number of individual howlers sighted per kilometer walked in combined data for years 1986–2012 versus number of individual howlers sighted per kilometer walked for 2011 and 2012, Barro Colorado Island, Panama.

evidence of disease found). Cool wet conditions typically characterize the late rainy season on BCI every year. Minimum daily temperature in December 2010 was lower than average for December due to the high rainfall and on 2 days dipped to 20.8–20.9°C. Daily variation in body temperature under constant laboratory conditions for *Cebus* spp. is on the order of several degrees Celsius, suggesting that environmental variation in air temperature of comparable magnitude can easily be buffered [Morrison, 1962]. Also, similar or even lower daily temperatures have been recorded for BCI in other months (e.g., July 2009), months that were not characterized by high capuchin mortality. Furthermore, montane *C. capucinus* populations are found up to 2,100 m in much colder thermal environments [Macdonald, 2001], providing further indirect evidence that hypothermia was not a primary factor in the BCI capuchin mortality event.

We hypothesize that the unusually high rainfall in 2010, particularly in December, largely eliminated the arthropod peak expected in December [Oppenheimer, 1982; Smythe, 1982; Worthington, 1982]. With few arthropods available, it is probable that many capuchins could not find sufficient dietary protein to survive. In December, birds' eggs, nestlings, or young mammals are scarce or absent. Some nuts and seeds can be valuable protein sources but no palm nuts or edible seeds occur in lists of the top five food items utilized by

BCI capuchins in either Mitchell's [1989] or Oppenheimer's [1982] multi-year feeding data for November or December. Oppenheimer's graph [1982, p. 262] of diet composition by month shows that in November, for the plant food portion of the diet, fruits comprised around 60% of capuchin feeding records while "new growth" (young leaves and shoots) and flowers and flower buds *each* made up around 20%. In Oppenheimer's December data, fruits made up around 50% of the plant food portion of the capuchin diet while the other 50% was *entirely* flower buds. Many flowers and flower buds are good protein sources [Milton, 1980; Rothman et al., 2006; Silver et al., 2000]. Oppenheimer's [1982] data also show that in November and December, the percent of feeding records capuchins devote to plant source foods declines notably while the percent of feeding records devoted to animal source foods rises in November and reaches its annual peak of >40% in December—this peak due to arthropod foods [Oppenheimer, 1982, Fig. 4, p. 257; see also Mitchell, 1989, p. 174]. The arthropod peak in December would supply capuchins with a valuable source of high quality protein, reducing their need to try and satisfy this essential requirement with new growth, flowers, and flower buds.

Feeding records therefore support our contention that BCI capuchins are particularly interested in proteinaceous foods in November and December. Multi-year data show that on BCI, arthropod consumption increases in November and December [Oppenheimer, 1982] as does the intake of proteinaceous plant parts [Mitchell, 1989; Oppenheimer, 1982]. Capuchin monkeys have very little volume in the cecum and colon [Hladik, 1967]. Indeed, the entire capuchin hindgut makes up only some 7.5% of total gut volume while the small intestine makes up 81%. This pattern of gut proportions indicates that capuchins are heavily dependent on high quality foods, amenable to digestion primarily in the small intestine. These facts, in combination with capuchin body size and rapid turnover of ingesta [Milton, 1984] make it unlikely that capuchin monkeys could satisfy daily protein demands with shoots, flower buds, and similar plant matter.

Mitchell [1989] hypothesized that the increasing dependence of capuchins on arthropod foods as the rainy season progresses is due to a decline in the quality of the fruit portion of their diet. In her view, by increasing their intake of arthropod foods, BCI capuchins are able to compensate for the decline in fruit quality. Similarly, Oppenheimer stated: "It is the smaller postmonsoon peak in arthropods during December and January [Smythe, 1974] that is important to the capuchins" [Oppenheimer, 1982, p. 205]—far more so than the major peak in arthropod abundance each year in the early rainy season because at that time, high quality fruits are also abundant. The December arthropod peak is also hypothesized to be important to other BCI vertebrates. Worthington [1982], for example, speculated that the December arthropod peak might cue breeding activities in BCI manikins. If edible arthropods were in unusually short supply in December/January on BCI and there were no other viable protein sources, we predict many capuchins would rapidly experience negative nitrogen balance, with the ensuing cascade of debilitating metabolic consequences predicted for insufficient dietary protein [Wardlaw & Insell, 1996]. If the December–January diet was also deficient in energy, this would only exacerbate any protein deficiency.

Captive trials on protein deprivation (<6% protein in the diet or protein lacking histidine/arginine) in common marmosets (*Callithrix jacchus*) showed that by day 4, monkeys began ingesting their fecal matter to secure any protein it contained [Flurer & Zucker, 1988]. This indicates that physiological effects of inadequate dietary protein are rapidly experienced by small monkeys and that continued deprivation for >72 hr can induce an extreme behavioral response [Flurer & Zucker, 1988]. Experiments on pregnant female squirrel monkeys (*Saimiri oerstedii*) fed different levels of protein showed that the incidence of abortion increased significantly on low protein diets (8% of calories from a protein source). When a fetus was aborted, the protein-starved female would avidly devour the placenta and fetus [Manocha & Long, 1977]. This cannibalistic behavior was not seen in females fed the high protein diet (=25% of calories from a protein source). These results likewise show that protein deficient diets can induce dramatic physiological/behavioral responses in monkeys.

In contrast to capuchins, howler monkeys on BCI generally do not deliberately include any animal source foods in their diet [Hladik, 1978; Milton, 1980]. Throughout the year, they rely heavily on young leaves for much of their dietary protein. Thus a lack of arthropod foods at any time of year should have no effect on howler numbers.

Though adult and infant capuchins likely also died in late 2010 to early 2011, none of their cadavers were recovered, indicating that mortality fell most heavily on the late juvenile to sub-adult age classes. We can suggest several reasons for this mortality pattern. As immature monkeys have not completed the growth process, they require more protein and energy per unit mass than adults; it would also be harder for maturing animals to lay down adipose stores. Consequently, immature capuchins should have lower fat reserves to draw on than adults and, if high quality foods were limited, should die earlier and in proportionately higher numbers than adults. *Cebus capucinus* is also characterized by a hierarchical social structure [Fragaszy et al., 2004; Perry, 1997, 2012]. This type of social structure suggests that lower ranking younger monkeys would likely be excluded from limited and contested dietary resources. Thus, in general, late juvenile and sub-adult capuchins would be predicted to do poorly under conditions of dietary stress and, if the dietary situation remained acute, should die earlier in disproportionately higher numbers than adults.

Recovered howler monkey cadavers were either extremely old or very young individuals. These age classes would be predicted to die earliest and in highest numbers in the late rainy season as this is the time of year when the howler diet is composed largely of leaves [Milton, 1980]. For leaf tissue to be fermented with maximum efficiency, leaves need to be reduced to small fragments. If not, fermentation efficiency is compromised and energy returns lower than those for monkeys effectively masticating their leafy foods. The old howlers found in late 2010 to early 2011 had molar teeth worn to the gum line; it would have been difficult to impossible for them to reduce leaves to small fragments. Very young howler monkeys would succumb because their small body size and a high leaf diet are not compatible—a very young howler monkey simply could not process enough leafy food per day to survive. Because lactation is energetically expensive and energy returns to howlers from fermentation are limited [Milton, 1979; Milton & McBee, 1983], by mid-December 2010, some female howlers with dependent offspring may have ceased to lactate. This too would negatively affect infant survivorship. Thus the mortality profile documented for howlers in late 2010 is precisely what would be predicted for this species whereas the capuchin mortality profile seems much harder to have predicted. These results show that the same natural disturbance can affect sympatric primate species in different ways, resulting in dramatically different mortality patterns.

Other BCI Mortality Events

The capuchin mortality event of late 2010 differs from all other accounts of primate or mammal mortality reported for BCI. The only other primate mortality event we are aware of in the past 40 years is one case of unusually high mortality documented for howler monkeys in 1989 [Milton, 1996]. This mortality appeared to result primarily from effects of an unusually heavy infestation by a parasitic bot fly specific to howler monkeys [Milton, 1996]. As this bot fly species parasitizes only howler monkeys, other primate species on BCI were not affected. Factors associated with the unusually heavy bot fly infestation of howlers in 1989 are not known. In 1958, there was an estimated 50% reduction in the island's coati (*Nasua narica*) population. Heavy rain in early 1958 is hypothesized to have drastically reduced the supply of leaf litter arthropods, the primary food of BCI coatis [Foster, 1982b].

At least two island-wide famines with high mammal mortality have been reported for BCI, one in 1931 and the other in 1970 [Foster, 1982b; Wright et al., 1999]. Both famines were attributed to the same factor—an island-wide shortage of edible fruits beginning in the middle of the famine year and continuing into the dry season of the subsequent year. Both fruit shortages are hypothesized to have resulted from some combination of climatic factors whose interactions are not yet well understood [Foster, 1982b; Milton et al., 2005; Wright et al., 1999]. In both cases, the famine year followed an El Niño year. In El Niño years, it is often the case that many tree species on BCI produce larger than average fruit crops with the result that in the following year, these same species or individuals often produce smaller than average fruit crops or even skip a year or 2 in fruit production [Foster, 1982b; Wright et al., 1999]. However, most El Niño years on BCI are not followed by years characterized by extreme fruit shortages and mammalian famines. Occasionally, an El Niño year is followed by a year with a short wet ["weak" *sensu* Foster, 1982b] dry season. On BCI, a short wet dry season may occasionally impact negatively on fruit production later that same year [Foster, 1982b; Milton et al., 2005; Wright et al., 1999]. Thus the combination of an El Niño year with high fruit production immediately followed by a year with a short, wet dry season could at times be associated with unusually low fruit production later in the second year, producing famine in the island's non-volant frugivores [Foster, 1982b; Milton et al., 2005; Wright et al., 1999]. A severe fruit shortage lasting over a period of months should impact all BCI primates, as three (capuchins, spider monkeys, tamarins) are highly frugivorous throughout the year and the fourth, howler monkeys, though able to survive for long periods on leaves, rely on fruit consumption earlier in the year to lay down fat stores to help cover energy demands when subsisting largely on leaves [Milton, 1980].

The best documented of the two BCI famines is that of 1970, as discussed by Foster [1982b], who fortuitously was studying fruit production on BCI prior to and during the famine period. 1969 was an El Niño year and 1970 was characterized by a short, wet dry season. Irrespective of the exact interplay of climatic and phenological factors, there was definitely a severe fruit shortage on BCI in the latter half of 1970, continuing into early 1971. The total dry weight of fruit per hectare falling into Foster's fruit traps between August 1970 and January 1971 was 63% lower than that during the corresponding period a year earlier [Foster, 1982b]. Many tree species that normally fruit during the second half of the rainy season, including many species important to BCI frugivores, simply failed to fruit. By July 1970, many BCI mammals were emaciated and showing obvious signs of hunger stress [Foster, 1982b]. Dead animals of many species were encountered increasingly often in the forest until by late November and December, "one could find at least one dead animal every 300 m along trails […]" [Foster, 1982b, p. 208]. Mortality was not quantified for any species during the famine period but, not surprisingly, many fruit-eating species with sizable populations (e.g., coatis, agoutis, peccaries, howler monkeys) were included in a list of the "most abundant" carcasses [Foster, 1982b, p. 208]. Without quantification, however, such data fall into the realm of anecdotal information and cannot be compared with the few quantitative data sets on mammal mortality by species, which exist for BCI in some years [e.g., Milton, 1990, 1996; Wright et al., 1999].

To our knowledge, no fruit shortages and associated mammalian mortality events of this magnitude have taken place on BCI since 1970. Wright et al. [1999] describe significant mortality for collared peccaries (*Pecari tajacu*) and white-tailed deer (*Odocoileus virginianus*) on BCI between September 1993 and February 1994 and attribute this mortality to a late rainy season fruit shortage in 1993. The event they describe, however, is minor in the extreme when compared to the magnitude of the 1970 famine event described by Foster [1982b]. K.M.'s skull collection data over the period September 1993 to February 1994, for example, do not show notable mortality for any primate species (i.e., a total of seven dead howlers in this 6-month period and no cadavers at all for the other three primate species; K.M., unpublished data).

Our data suggest that fruit availability on BCI in the latter half of 2010 differed both from the severe island-wide fruit shortage of 1970 and the lesser fruit shortage of 1993. 2010, like 1970 and 1993, followed an El Niño year and had a dry season that was wetter than average, but until the latter half of December 2010, there is no evidence to suggest that primates or other frugivorous mammals were dying in unusual numbers from famine as evidenced by the fact that remarkably few dead mammals were found in the forest until mid-December 2010. Nor do fruit trap data indicate a severe fruit shortage on BCI in late 2010 (J. Wright, personal communication to J.G.). If anything, prior to mid-December 2010, overall mortality of BCI mammals was lower than average, suggesting that for almost the entire year, most animals were able to secure sufficient food to sustain life. After December 9, however, capuchin cadavers were encountered in unprecedented numbers; cadaver reports indicate mortality of collared peccaries was also unusually high at this time (J.G., unpublished data).

Though dietary factors are implicated in the mortality experienced by both monkey species we believe that the foods involved differed for each. For capuchins, we hypothesize that the single most important factor was a lack of edible arthropods in December–January due to unprecedented high December rainfall. For howler monkeys, the extreme December rainfall appears to have extended the period of time they were forced to survive on high leaf diets with the result that some extremely old and very young howlers died.

2005 Primate Mortality Event in Costa Rica

BCI is not the only site in Central America to have recently experienced the notable decline of one or more primate species in association with extreme rainfall in the late rainy season. In late 2005, press accounts reported a notable die off of primates in Corcovado National Park, Costa Rica. This 550 km^2 nature reserve, contains four monkey species, squirrel monkeys (*Saimiri sciureus*) and the same species of spider, howler, and capuchin monkeys as found on BCI [Froehling, 2005]. Corcovado experiences seasonal rainfall patterns very similar to BCI, except that in the Corcovado region, both seasons are rolled back a month. At Corcovado in November (analogous to BCI in December), typically, the rains slack off and the dry season begins. 2004 was an El Niño year and in 2005, the Corcovado area experienced higher than average rainfall, such that November had double the average monthly rainfall. Park rangers remarked on the cool wet weather (G. Wong, personal communication to K.M., July 2012) and dead animals, largely monkeys, began to appear in "alarming numbers" in late 2005 [Froehling, 2005]. Little quantification of mortality for any species is available as Costa Rican scientists only became aware of unusually high mortality when the event was almost over. By late November 2005, one Costa Rican researcher estimated that ultimately perhaps as many as 30–40% of the park's monkeys had died [Rosner, 2006]. Initially, a virulent disease, possibly yellow fever, was hypothesized to be associated with the primate deaths, but tissue samples from Corcovado spider monkeys (the most affected species) showed no evidence of disease [Rosner, 2006]. Blood samples from 12 monkeys (species not identified) showed hematocrit and hemoglobin values lower than those in "normal" captive animals (G. Wong, personal communication to K.M., July 2012). Necropsy of a spider monkey and a capuchin revealed extreme malnutrition and high internal parasite loads (G. Wong, personal communication to K.M., July 2012). The rainy weather in 2005 was hypothesized to have interfered with fruit production, causing famine in the monkey populations [Froehling, 2005]. It was concluded that affected animals had starved to death due to a lack of suitable foods and an inability to forage for food during several months of unusually high rainfall and cool weather [Rosner, 2006; G. Wong, personal communication to K.M., July 2012]. Interestingly, while the monkeys were dying, terrestrial mammals in the park such as coatis, pacas, and peccaries appeared unaffected; in 2006, in spite of the apparent dietary hardship in late 2005, many new infants were seen in all four monkey populations (G. Wong, personal communication to K.M., July 2012).

Implications for Conservation

Much attention today, in this era of global warming, is given to discussion of climatic events, particularly El Niños. Though El Niño events affect the weather worldwide, our data show that the environmental impact of a specific El Niño, even in a single geographical region (e.g., the region of Central America encompassing Panama and its neighbor, Costa Rica) appears to affect different sites in different ways. For example, fruit scarcity and high primate mortality were not noted for BCI in 2005 or for Corcovado in 2010. Barring large-scale environmental catastrophes, it would appear that in terms of natural disturbances, each site must be examined largely in terms of itself. When environmental disturbances such as high annual rainfall or heavy rainfall at an unexpected time of year do occur, many additional factors appear to come into play to determine which food sources will be affected and which mammal species will suffer as a result. In one case, a severe fruit shortage may negatively impact many different species at a given site (e.g., 1970 famine on BCI; 2005 event at Corcovado); in another case, only one or two species may be strongly affected (e.g., 1994, deer and peccaries on BCI; 2010, capuchin monkeys and peccaries on BCI).

Long-term data from BCI suggest that even in so-called "normal" years, it may be difficult to predict how annual rainfall will affect fruit production and population fluctuations of resident frugivores. In 2005, Milton et al. compared rainfall, ripe fruit production and population estimates for two primate species—howler monkeys and capuchin monkeys—and two rodent species—agoutis and red-tailed squirrels—over a 15-year period for BCI. All four species consume considerable fruit. Fruit production showed no correlation with rainfall, either within years or when rainfall was lagged back 1 or 2 years relative to the year of fruit production [Milton et al., 2005]. Population estimates for each mammal species showed interannual fluctuation, at times notable, but these fluctuations did not appear to track fruit production estimates either within years or when tested with a 1- or 2-year lag [see Milton et al., 2005 for details]. Nor did population estimates for closely related species necessarily track together in relation to fruit production estimates—within the same year, howlers and capuchins often showed divergent population patterns as did agoutis and squirrels. Overall, combined results suggest that population fluctuations for each species are likely influenced by a constantly varying combination of factors and that, excluding rare catastrophic environmental events, the factors affecting the population dynamics of one species in a given year may not necessarily impact similarly on another species in that same year at that same site [Milton et al., 2005].

Information presented in this paper suggests that our current knowledge about basic factors related to effects of natural disturbances on fluctuations in the population parameters of primates is limited. Considerably more long-term knowledge of dietary ecology, along with similar information on population parameters by season and by year over a period of years, seem required to make reliable predictions about the outcome of climatic disturbances on species targeted for conservation efforts. Additionally, such data need to be combined with rainfall and other environmental parameters and their effects on phenological production patterns of both primary and fallback dietary resources that fulfill the nutritional requirements of each target species. We suggest that more long-term research at several comparative sites be devoted to this timely and increasingly important topic.

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