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Climate oscillations and conservation measures regulate white-faced capuchin population growth and demography in a regenerating tropical dry forest in Costa Rica

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ABSTRACT

Tropical dry forests are among the world's most imperiled biomes, and most long-lived and large-bodied animals that inhabit tropical dry forests persist in small, fragmented populations. Long-term monitoring is necessary for understanding the extent to which such populations can cope with changing climate conditions and recover after the elimination of human disturbances. We investigated how conservation measures, local rainfall patterns, and large-scale climate oscillations have affected the population dynamics of white-faced capuchins (*Cebus capucinus*) in a Costa Rican tropical dry forest over a 42-year period after the elimination of most human disturbances. The population's rapid initial growth and later stabilization suggests that it was below the habitat's carrying capacity at the time of the conservation area's establishment. Management practices, such as aggressive fire suppression, may have played an important role in promoting this growth. Rainfall patterns were strongly coupled with phases and intensity conditions of the El Niño Southern Oscillation. The population experienced two distinct growth phases after the conservation area's establishment, a period of rapid growth through the 1980s and 1990s and a subsequent period of stability from about 2000 to the present. El Niño-like conditions in the three years preceding a census year were associated with declines in reproductive output and/or offspring mortality during the rapid growth phase. The sensitivity of this ecosystem to global climatic phenomena suggests that some animals will be negatively affected if drought years become more common as the global climate warms.

1. Introduction

Long-term monitoring is vital for understanding the biological requirements and conservation outlook of threatened animal populations (Clutton-Brock, 2012; Sinclair and Byrom, 2006). A major aim of long-term population monitoring is to describe trends in demographic variables over time (Clutton-Brock and Sheldon, 2010). By documenting such trends, it may be possible to link population fluctuations with changes in climate and habitat (Wright, 2007), thereby improving predictions about how the population will fare in projected disturbance or climate change scenarios (Lawler et al., 2006). The demographic structure of relatively small or isolated populations may be especially sensitive to anomalous events such as human disturbance, natural disasters, prolonged extreme climatic episodes, and disease outbreaks. These dependencies may be impossible to detect without concurrent and systematic data on climate and population trends over a multi-generational time frame (Clutton-Brock, 2012). Most studies of long-lived nonhuman primates have not been lengthy enough to investigate these important questions, and consequently, there have been few studies on the long-term dynamics of primate populations in relation to quantitative data on ecosystem change (for some notable exceptions, see chapters in Kappeler and Watts, 2012). Nonetheless, primate taxa may be particularly useful for quickly gauging conservation risks and establishing conservation priorities because primates are often abundant and easily censused compared to many other vertebrates in tropical habitats, and they may play key roles in ecological communities as ecosystem engineers (Chapman et al., 2013). Conservation approaches focused on primates are therefore likely to confer protection to many other sympatric organisms and their ecological dependencies (Lambert, 2011).

With few exceptions (e.g. Robbins et al., 2011; Strier and Boubli, 2006; Strier and Ives, 2012), our current knowledge about the long-term effects of climate and ecosystem change on primates comes from declining populations of lemurs (Dunham et al.,

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2011; Jolly, 2012; Sussman et al., 2012; Wright et al., 2012) and Old World monkeys (Chapman et al., 2010, 2005, 2000; Lwanga et al., 2011). Thus, most studies on primates' responses to environmental change have focused on their capacity to cope with diminishing and/or deteriorating ecosystems. This focus pragmatically reflects the dire situation faced by many primate populations around the world (Cowlishaw and Dunbar, 2000). However, it is also important to know how primate populations fare in conservation areas that are "succeeding" (Laurance et al., 2012); that is, areas in which the major anthropogenic detriments to primates—deforestation, logging, live-capture, hunting, and fire (Chapman and Peres, 2001)—have been effectively and lastingly eradicated. Conservation strategies that target large, long-lived animals in profoundly disturbed habitats may be predicated on the belief that dwindling populations will recover over time if their habitats can be adequately restored. Globally, there are very few study sites that both support primates and meet the reserve-health criteria for investigating these important questions, and even fewer sites with a sufficiently long record of continuous demographic, climatic, and ecological monitoring to draw meaningful conclusions.

Several studies that have examined the dynamics of primate populations have implicated global weather patterns as a key driver (Dunham et al., 2011, 2008; Milton and Giacalone, 2014; Wiederholt and Post, 2011, 2010). The El Niño Southern Oscillation (ENSO) is one of the most globally consequential large-scale climate oscillators: extreme phases of ENSO have geographically widespread and diverse effects on local weather. Although relatively few studies have examined the effects of ENSO phases on nonhuman populations, there is evidence from geographically widespread locations that extreme ENSO phases can trigger significant population dynamic events, including changes in fecundity and mass mortality. For example, warm phases of ENSO ("El Niño") are associated with reduced fecundity in Milne Edward's sifaka (*Propithecus edwardsi*), perhaps due to the greater severity of cyclones that strike Madagascar during such periods (Dunham et al., 2011, 2008). El Niño phases also coincide with or closely precede synchronous population declines, delayed birth seasons, and reduced birth rates in various geographically-dispersed primates of the Neotropical family Atelidae, perhaps due to the disruption of food tree phenology (Wiederholt and Post, 2011, 2010). Extraordinarily high rainfall associated with strong episodes of the cool phase of ENSO ("La Niña") may have been responsible for a mass mortality event among the white-faced capuchins (*Cebus capucinus*) on Barro Colorado Island, Panama (Milton and Giacalone, 2014). In light of these widespread and diverse effects on primate populations, there is an urgent need to assess the risks that large-scale climatic oscillations pose to primates in order to make informed conservation decisions.

Here, we examine demographic changes of a population of white-faced capuchins (*Cebus capucinus*) in northwestern Costa Rica over a 42-year period in relation to local weather patterns and large-scale climate oscillations during the same period. Previous studies have documented the rapid growth of this capuchin population since the early 1970s (Fedigan, 1986; Fedigan et al., 1996, 1985; Fedigan and Jack, 2012, 2001; Freese, 1976). These studies indicate that the population was well below its carrying capacity when the conservation area was established, and they point to the elimination of fire damage and other anthropogenic detriments as the key conservation measures that enabled this growth (Fedigan and Jack, 2001). The study area is situated in the core of a well-studied and thriving endeavor in ecosystem restoration that was initiated in 1971 (Allen, 2003; Janzen, 2000, 1987; Woodworth, 2013). Our study offers a unique perspective on the factors that promote or limit primate population growth, and it sheds light on their potential for recovery after the elimination of human disturbances. Our objectives are to: (1) describe historical trends in our study site's population of capuchins from 1971 to 2013, extending previously published records (Fedigan, 1986; Fedigan et al., 1996, 1985; Fedigan and Jack, 2012, 2001; Freese, 1976); (2) assess the relationship between local rainfall patterns and indices of large-scale climate oscillations; and (3) model the relationship between population trends and both local and large-scale climate patterns.

2. Materials and methods

2.1. Study System

Our study area is Sector Santa Rosa (SSR) of the Área de Conservación Guanacaste (ACG) in northwestern Costa Rica (10.84°N, 85.62°W), a UNESCO World Heritage site and a global model of tropical dry forest restoration ecology (Allen, 2003; Janzen, 1987). Janzen (2000) gives a thorough history of the anthropogenic disturbance of this region, the creation and expansion of the ACG, and the ecological recovery that has occurred after decades of aggressive fire suppression. Land owners in the Guanacaste province of Costa Rica set fires annually to manage overgrown cattle pastures, and throughout the 1970s and early 1980s (and presumably for centuries before), these fires routinely swept into the park and burned large tracts of forest (Janzen, 2000). Since the park's founding, there were nascent efforts to limit fire damage, but effective fire control was not realized in SSR until 1984 (Janzen, 1988). Subsistence hunting of white-faced capuchins is historically uncommon in Costa Rica (Gonzalez-Kirchner and Maza, 1998) and is absent today in SSR, but capuchins (particularly capuchin males) probably faced regular harassment by ranchers before SSR's establishment (Fedigan and Jack, 2001). The ACG was classified as "succeeding" in a recent global assessment of 60 representative tropical forest reserves, ranking second in overall reserve health (Laurance et al., 2012). The geographic boundaries of SSR, which contain 108 km^2 of varied habitat, were formed with the establishment of Santa Rosa National Park in 1971. SSR is situated in a dry tropical forest biome that experiences stark rainfall seasonality, with nearly all the annual rain falling between mid-May and late-November. The 6-month-long dry season triggers total leaf shedding in many plant species. SSR supports three primate species, the white-faced capuchin, the mantled howler (*Alouatta palliata*), and the black-handed spider monkey (*Ateles geoffroyi*). This paper focuses on the population of white-faced capuchins.

2.2. Data collection

2.2.1. Park-wide censuses

The population demographic data consist of 14 censuses carried out between 1971 and 2013 (Fedigan, 1986; Fedigan et al., 1996, 1985; Fedigan and Jack, 2012, 2001; Freese, 1976). Most of the censuses were carried out between late April and June, a time period that corresponds to the dry-to-wet season transition in SSR. Beginning with the 1983 census, teams of observers employed a "modified quadrat" technique in which separate pairs of searchers walked transects and all trails, roads, fence lines, and stream beds in a chosen sampling area. Any capuchins encountered were followed until multiple observers could agree on a consistent, complete group count and composition, or until the group was lost. Distinctive individuals in each group were described (e.g., those with noticeable scars, pelage markings, or missing digits/tail portions), and these notes were used to avoid repeat counts of the same group. In later years, straight-line transects were discontinued as census-takers became increasingly proficient at relocating