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Successional loss of two key food tree species best explains decline in group size of Panamanian howler monkeys (*Alouatta palliata*)

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Abstract

Negative impacts of discrete, short-term disturbances to wildlife populations are well-documented. The consequences of more gradual environmental change are less apparent and harder to study because they play out over longer periods and are often indirect in their action. Yet, they can drive the decline of wildlife populations even in seemingly pristine and currently well-protected habitats. One such environmental change is a successional shift in a community's species composition as it regenerates from disturbance caused by past human land use. Early and middle successional tree species often provide key foods to folivores and frugivores, but the abundance of these resources drops as the forest matures, with adverse repercussions for these consumers. Our 44-year record (1974–2018) of howler monkey (*Alouatta palliata*) group sizes and demographic composition from Barro Colorado Island, Panama, a protected reserve, documents an example of this phenomenon. After 70 years of relative stability, the mean size of howler monkey groups exhibited a marked decline, beginning in 2003. This downward trajectory in group size has continued through the most recent census in 2018. The composition of howler groups also changed significantly during the study period, with the patterns of decline differing among age/sex classes. There is no evidence that these changes were caused by increased rates of emigration, group fission, predation, parasitism, or disease. Rather, they are best explained by an island-wide, succession-driven decline in the densities of two species of free-standing fig trees, *Ficus yoponensis* and *F. insipida*, which together were providing ~36% of BCI howlers' annual diet.
Abstract in Spanish is available with online material.

KEYWORDS
Alouatta palliata, *Ficus* spp., food limitation, group size, howler monkey, Moraceae, primate population dynamics, tropical forest succession

1 | INTRODUCTION

From 1970 to 2012, a period of <50 years, population sizes of wild vertebrate species are estimated to have dropped an average of 58% globally, a decline that is predicted to grow to 67% by the end of this decade (World Wildlife Foundation, 2016). In many instances, the losses are caused by the immediate negative impacts of localized human activities, such as hunting and habitat alteration/destruction, on rates of wildlife reproduction and survival (e.g., Burbidge & McKenzie, 1989; Corlett, 2007; Daszak, Cunningham & Hyatt, 2000,

2001; Harrison, 2011; Johns & Skorupa, 1987; Peres, 2000, 2001; Peres & Palacios, 2007; Robinson, Redford & Bennett, 1999). Of equal and increasing concern are more gradual, larger-scale changes in climate and associated disturbance regimes that can directly or indirectly lead to the reduction or eradication of wildlife populations even in seemingly pristine or well-protected habitats (Chapman et al., 2010; Grosbois et al., 2008; Laurance et al., 2012; Milton & Giacalone, 2014). In addition, there can be important, albeit less apparent, legacy effects of past human land-use practices that may not manifest for decades following cessation of the habitat-damaging activities. For example, successional changes in vegetation structure and species composition following abandonment of agricultural lands in the northeastern U.S. led to large changes in bird species composition and diversity decades later (Dettmers, 2003; Hunter, Buehler, Canterbury, Confer & Hamel, 2001; Litvaitis, 1993).

The most egregious drop in wildlife numbers appears to be taking place in the tropics (Peres, 2001; Stoner, Vulinec, Wright & Peres, 2007; World Wildlife Foundation 2014). This includes some 50% of extant primates, almost all of which are arboreal and confined to tropical forest habitats, which are now considered endangered, due in large part to the effects of anthropogenic factors such as logging and the bush meat trade on their populations (Abernethy, Coad, Taylor, Lee & Maisels, 2013; Brashares et al., 2004; Chapman, Balcomb, Gillespie, Skorupa & Struhsaker, 2000; Fa, Peres & Meeuwig, 2002; Linder & Oates, 2011; Michalski & Peres, 2005; Milner-Gulland et al., 2003; Peres, 2000; Ripple et al., 2016; Wilkie & Carpenter, 1999). However, there have been few long-term studies capable of rigorously evaluating the impacts of more gradual environmental changes on primate demography, particularly in tropical forests (e.g., Chapman et al., 2010; Clutton-Brock, 2012; Fedigan & Jack, 2012; Lwanga, Struhsaker, Struhsaker, Butynski & Mitani, 2011; Milton & Giacalone, 2014; Morris et al., 2011; Pusey, Pintea, Wilson, Kamenya & Goodall, 2007).

Here, we examine population characteristics of free-ranging, mantled howler monkeys (*Alouatta palliata*) living in tropical forest on Barro Colorado Island (BCI), Panama. Howler monkey populations are organized into discrete groups, which are largely closed social systems (Milton, 1980). The average size of BCI howler groups remained remarkably stable at 17–23 individuals over the 70 years from 1932 to 2001. Censuses conducted by Carpenter in 1932, 1933, and 1959 recorded essentially the same mean group size that Milton documented between 1974 and 2001 (Carpenter, 1934, 1962; Milton, 1982, 1996; Milton, Giacalone, Wright & Stockmayer, 2005; Ryan, Starks, Milton & Getz, 2008).

This paper extends the span of published BCI howler monkey group censuses conducted by Milton to cover 44 years (1974–2018). The added census records indicate a marked decline in the average size of howler groups, beginning in the early 2000s. We statistically evaluate this apparent downturn and assess whether the trend continues. We also analyze changes in the demographic composition of groups over the entire census period. Lastly, using average group sizes and new island-wide group counts, we update previously published estimates of the total size of the BCI howler population.

A variety of phenomena might cause a drop in average group size, including increased emigration of howlers from the island, fission of groups in response to social factors, including intra-group resource competition (Dittus, 1988), an increased rate of predation, a rise in incidence of a lethal disease or macroparasitic infection, or a decline in food resources leading to heightened competition and lower reproduction and/or survival. We use a variety of quantitative and qualitative information to evaluate these alternate explanations for the observed changes in group size and composition.

2 | METHODS

2.1 | Study site

BCI (lat: 9.1543, long: −79.8461) was formed in 1914 after the Chagres River was dammed to create Gatun Lake, the central segment of the Panama Canal passage. This 15.6 km^2 island was designated a protected nature reserve in 1923. Different parts of the island had experienced distinctly different histories of human-caused disturbance prior to it becoming a reserve. The southwestern half of BCI has been largely undisturbed for several centuries and is covered in old-growth forest (Albrecht, Stallard & Kalko, 2017; Foster & Brokaw, 1982; Hubbell & Foster, 1986; Leigh & Wright, 1990; Piperno, 1989). In contrast, much of the northeastern half of BCI experienced disturbance from canal-construction or agriculture-related activities prior to 1923 (see Fig. 2 in Albrecht et al., 2017). When the island gained protected status, disturbance associated with these activities ceased and the forest in impacted areas began to regenerate. Today, the entire island is covered in Tropical Moist Forest (Holdridge, Grenke, Hatheway, Liang & Tosi, 1971) and consists of a mosaic of old-growth forest, undisturbed for at least 400–500 years, and second-growth forest, now approaching 100–150 years in age. Since the island became a reserve, the BCI forest has experienced little anthropogenic influence; other than the effects of isolation in limiting biotic exchange with the mainland, there has been no hunting pressure, forest cutting, or other forms of localized human-caused disturbance.

2.2 | Study species

2.2.1 | Howler monkey home range, diet, and feeding behavior

Each howler group lives within a clearly defined home range area, which on BCI is ~30 ha in size (Milton, 1980). A given howler group does not have exclusive use of its home range. Rather, there is extensive home range overlap, each group typically sharing portions of its home range with three or more neighboring groups (Hopkins, 2011; Milton, 1980).

The howler diet consists of young leaves and ripe fruits, supplemented with flowers, flower buds, and petioles, taken from a wide variety of tropical forest trees and vines (Carpenter, 1934; Glander, 1978, 1981; Hladik & Hladik, 1969; Milton, 1978, 1980). On BCI, howlers take foods from more than 130 different plant species per

TABLE 1 Percent of time howlers spent feeding at different fruit tree species in old-growth (Old Forest) and secondary forest (Lutz Catchment[a]) stands on BCI (data from Milton, 1980, pp. 67–70, with corrections). Species that ranked in the top 12 in % feeding time at each site are reported. Dietary resources supplied by each species include fruit (F), leaves (L), flowers (Fl), and/or petioles (P)

Fruit tree species	Dietary resource	Old forest rank	% feeding time	Lutz Catchment rank	% feeding time
Ficus yoponensis	F, L	1	15.32	1	25.95
Brosimum alicastrum	F, L	2	11.25	7	1.48
Ficus insipida	F, L	3	5.91	2	22.88
Cercropia insignis	F, L, Fl, P	4	3.44	10	0.96
Hieronyma alchorneoides	F, L	5	3.23		
Ficus costaricana	F	6	1.99		
Quararibea asterolepis	F, L	7	1.86		
Anacardium excelsum	F, L	8	1.79	9	1.19
Trichilia tuberculata	F, L	9	1.50		
Eugenia oerstediana	F, L	10	1.46		
Chrysophyllum argenteum	F	11	0.96		
Dipteryx oleifera	F	12	0.91		
Spondias radlkoferi	F, L			3	4.96
Lacmellea panamensis	F			4	3.16
Pterocarpus rohrii	F, L, Fl			5	2.48
Maquira guianensis	F, L			6	1.59
Ficus trigonata	F, L			8	1.41
Eugenia coloradensis	F, L			11	0.74
Socratea exorrhiza	F			12	0.49

[a]Milton (1980) refers to this site as Lutz Ravine.

year. Because fruits represent the greatest source of ready energy for howlers (Milton, 1980), our assessment of the role of food limitation in causing the observed decline in average group size focuses on changes in the numbers of large fruit trees. Howler groups occupying areas of BCI with different forest tree compositions feed on somewhat different suites of fruit tree species (Table 1). Yet, their feeding activity is concentrated on four tree species that rank among the top three sources of fruit foraged by howlers in old-growth and/or secondary forest habitats: *Ficus yoponensis*, *F. insipida*, *Brosimum alicastrum* (all members of Moraceae), and *Spondias radlkoferi* (Anacardiaceae) Over the annual cycle, howlers devote 32% and 55% of their feeding time to consuming the fruits of these four species in the old-growth and secondary stands, respectively. By comparison, they spend < 4% of their feeding time on any other fruit species (Table 1).

Fruit production (g dry fruit matter per fruit crown volume) increases with a tree's diameter at breast height (DBH; Chapman et al., 1992; Miller & Dietz, 2004), so the abundance of larger trees is a good indicator of overall fruit abundance (Chapman et al., 2010; Chaves, Stoner & Arroyo-Rodríguez, 2012). Large trees provide the bulk of howler food resources on BCI (Carpenter, 1934; Milton, 1980). The DBH of major foraging trees is about 55 cm (Hopkins, 2008). When a large tree is producing ripe fruits, it often yields far more fruit than any one howler group can consume. Under these

circumstances, the home ranges of neighboring howler groups will overlap, as they elect to share use of such large food trees rather than expend often limited energy trying to defend an exclusive territory (Milton, 1980). Therefore, the death of even a single large fruit-producing tree can markedly lower the biomass of fruit available to several howler groups in a given area of forest. Moreover, large trees comprise the primary routes of lateral foraging movements through the forest canopy, and howler groups repeatedly use certain arboreal pathways (Garber & Jelinek, 2005; Hopkins, 2008, 2011; McLean et al., 2016; Milton, 1980). Alteration of these pathways affects group day ranges and may substantially increase the energetic demands of group members.

2.2.2 | Life histories of howlers' preferred fruit tree species

The free-standing figs, *Ficus yoponensis* and *F. insipida*, possess numerous life history traits typical of pioneer species: their fruits contain large numbers of very small seeds, seed germination, and seedling establishment and persistence require high light conditions, and the trees are very fast growing in open conditions or once they enter the canopy layer (Banack, Horn & Gawlicka, 2002; Foster, 1986, 1990; Knight, 1975; Terborgh, Flores, Mueller & Davenport, 1997). Consistent with these life history traits, the density of large

free-standing figs is typically highest in secondary forest that has grown up following past disturbances that created the open conditions necessary for recruitment. As mentioned above, this forest type predominates in the northeastern half of BCI. The abundances of the free-standing figs, *Ficus yoponensis* and *F. insipida*, peak toward the middle of a successional sequence and decline markedly as the secondary forest matures (Foster, 1986, 1990; Guariguata & Ostertag, 2001; Terborgh et al., 1997). On BCI, their numbers have dwindled as secondary forest stands reached 90–150 years of age (Albrecht et al., 2017), reflecting the ~100-year life spans of these two *Ficus* species (Milton et al. 1994).

Like the two species of free-standing figs, *Spondias* spp. are considered pioneer tree species found in greatest number within secondary forest (Janzen, 1985; Knight, 1975; Lang & Knight, 1983; Rüger, Huth, Hubbell & Condit, 2009). Milton (1980, pp. 67–70) observed howlers feeding on *S. radlkoferi* in her secondary, but not old-growth, forest study site on BCI. In contrast, large, mature individuals of *Brosimum alicastrum* are most abundant in old-growth forest stands.

2.3 | Field sampling protocols and data analyses

2.3.1 | Howler group censuses

Annual censusing to determine howler monkey group size and composition was begun by Katharine Milton (KM) in 1974 and has been continued by her to the present. Censusing is carried out one, two or, occasionally, three, or more times per year. In each census, KM walks trails on BCI in all parts of the island for 7–10 consecutive days and whenever a howler group is encountered or heard within an accessible distance, the group is located, examined with binoculars, and all individuals in it are counted, aged, and sexed, if the individual is mature (Milton, 1982, 1996; Milton et al., 2005). The total number of groups counted in a census can vary as, at some times of year, especially mid-late rainy season, howler groups are harder to locate and fewer groups are encountered over the census period. For a given census to be included in the data set, a minimum of five groups from different areas of the island had to have been counted, but generally 10 or more groups are counted per census. Identification categories used in each census included: infant (birth to ~12 months of age), juvenile (~12–60 months of age), adult female, and adult male (Milton, 1996).

We fit standard and piecewise generalized linear models (GLMs) to the census count data to determine whether the recent hypothesized decline in howler monkey group size significantly deviated from historical mean counts. For all models, we used the month-year date of each census as the independent variable. Because our data were discrete integer counts, we compared GLM models in the Poisson and negative binomial families, which differ in the numbers of parameters required by each distribution (1 and 2, respectively). We anticipated that models with a negative binomial error distribution, with their separate overdispersion parameter (theta), would provide better fits to the data. This expectation was confirmed in preliminary analyses, so we only report results for the negative binomial models here.

We compared models with constant means (intercept-only), variable means (with a single intercept and slope), and piecewise slopes (with a single intercept and multiple slopes at different time points). Piecewise regression models fit separate regression segments over partitioned intervals of the independent predictor variable. Therefore, the method can be used to detect abrupt shifts or thresholds in time series data (Toms & Lesperance, 2003). In this procedure, at least two additional parameters are estimated: one or more breakpoints (ψ_i) and their associated slope parameters (β_i). To avoid overfitting, we constrained the maximum number of breakpoints to one per model. We used the R v. 3.31 (R Development Core Team 2016) software package segmented v. 2.1 (Muggeo, 2008) to fit both Poisson and negative binomial piecewise and standard GLMs to the group counts over the census period from 1974 to 2018. In addition, we fit null intercept-only GLMs to test for an overall effect of time on mean group counts. Best-fit GLM models were selected using deviance-based fit metrics ("pseudo-R^2") (Nagelkerke, 1991) and Akaike's information criterion (AIC) (Anderson, 2008; Burnham & Anderson, 2002; Burnham, Anderson & Huyvert, 2011). We computed ΔAIC values to estimate the distances between the selected or "best" model and ranked alternative models, and applied a relatively conservative criterion to model discrimination, interpreting any ΔAIC value < 7.0 as indicating equally parsimonious models (i.e., an evidence ratio of < 33:1). For piecewise models, Davies' test was used to evaluate the null hypothesis of equal slopes on either side of ψ (Davies, 1987). This procedure was repeated for each demographic group (adult males, adult females, juveniles, infants). We also examined temporal trends in the ratios of immatures (infants + juveniles) to adult female and infants to adult female, using the same modeling procedure, but treating these values as Gaussian-distributed.

Temporal autocorrelation among census counts, which can bias GLM fit, was not detectable in our data (Appendix S1: Figure S1).

2.3.2 | Estimates of island-wide howler population size

Previously published estimates of the total number of howlers living on BCI were made in 1933 (Carpenter, 1934, 1965), 1951 (Collias & Southwick, 1952), 1959 (Carpenter, 1962, 1965), 1970 (Mittermeier, 1973), 1974, 1977, 1978 (Milton, 1982), and 1988 (Milton, 1996). We extended this record using new island-wide group counts made by KM and teams of 25–36 field assistants in 1997, 2006, and 2010. Total population size was estimated by multiplying these island-wide group counts by the average group size, calculated from contemporaneous membership tallies of multiple groups across the island. The procedure for locating and mapping groups was the same as KM has employed in past island-wide surveys (see Milton, 1982, p. 275 for details). The observers are positioned at roughly evenly spaced stations across the island, most along the island's 39.5 km trail system, but some are transported by boat to locations on the periphery of the island that have no trail access. These island-wide counts are generally conducted over two consecutive days; the 2006 survey was limited to a single day. These efforts detected howler groups

all across the island (e.g., see Fig. 1 in Milton, 1982) for a map of the spatial distribution of groups counted in her 1977 survey).

2.3.3 | Abundance of large fruit trees

Our examination of temporal changes in large fruit tree abundance on BCI focused on the four species most heavily fed upon by howlers: *Ficus yoponensis, F. insipida, Brosimum alicastrum,* and *Spondias radlkoferi*. The most comprehensive data on the abundances of the two free-standing figs on BCI were summarized by Albrecht et al. (2017) and come from two complementary long-term monitoring studies. One of these focused on a 25-ha plot in the Lutz Catchment in the northeast quadrant of BCI (see Fig. 2 in Albrecht et al., 2017), one of the sites where Milton (1980) monitored howler monkey feeding behavior (Table 1). In 1973, 142 mature fig trees (≥ 50 cm DBH), comprised of six species, were individually tagged and their fates monitored at irregular intervals for 38 years, through 2011. The combined number of *Ficus yoponensis* and *F. insipida* trees represented 84% of the marked sample (71 and 48 individuals, respectively). The second set of long-term fig census data comes from an island-wide fig tree census begun in 1985 and continued at irregular intervals until 2009. Over the course of the study, more than one thousand fig trees, comprised of 16 species, were marked, mapped, and measured, all ≥ 50 cm DBH. Together, *Ficus yoponensis* and *F. insipida* represented about 70% of the mapped trees (470 and 365 individuals, respectively).

Counts of large *Brosimum alicastrum* and *Spondias radlkoferi* trees are only available from the 50-ha permanent forest plot that was established in 1980 by SP Hubbell and RB Foster on the central plateau of the island (Condit, 1995, 1998; Hubbell, Condit & Foster, 2015;; Hubbell & Foster, 1983, 1986) hereafter referred to as the BCI Forest Dynamics Plot (FDP). The forest within the plot is relatively old-growth, largely undisturbed by human activity for 200–400 years (Foster & Brokaw, 1982; see Fig. 2 in Albrecht et al.,

2017). The initial census of the plot was conducted between 1981 and 1983; it has been recensused at 5-year interval between 1985 and 2015. We tallied the numbers of large individuals (≥ 50 cm DBH) of *B. alicastrum* and *S. radlkoferi* occurring on the FDP at each census.

We inspected the census records of these four primary food tree species for evidence of any marked declines in numbers that immediately preceded observed changes in howler group size or composition.

3 | RESULTS

3.1 | Howler group size and age/sex composition

We detected statistically significant decreases in howler monkey group sizes beginning in approximately 2003 (Figure 1, Table 2). Before this period, mean howler monkey group sizes remained relatively stationary, fluctuating near a value of 18.7 (± 2.1 SD) individuals. These counts decreased to a mean of 11.9 (± 1.5 SD) for the period spanning 2015–2018 and fell to their lowest mean value of 10.8 in 2018. Similarly, we detected statistically significant downward breakpoints in the average number of adult females (Figure 2a) and infants (Figure 2c) per group in 2002, and in adult males (Figure 2b) and juveniles (Figure 2d) in 2004 (Table 2). The ratio of infants to adult females experienced a steady and significant decline over the entire census period (Figure 2e, Table 2). The ratio of immatures (infants + juveniles) to adult females also exhibited a steady decline over much of the study period, with what appears to be a steeper downturn in 2016, however, this recent breakpoint could be an end-of-record sampling artifact (Figure 2f, Table 2).

These changes in average group size and age/sex composition, which began in 2002–2004 and continued through 2018, are not an artifact of reduced sampling effort during that period. In fact, the average number of groups tallied per census from 2002 to 2018 (28 censuses) was greater than during the same number of years

FIGURE 1 Howler group counts over the 44-year census period. Each point is the total number of individuals in a censused group. The solid black line connects the median counts of each census. The red line is the best-fit, most parsimonious regression model and the vertical dashed line is the estimated break point for piecewise regressions. See Table 2 for model estimates and statistical results
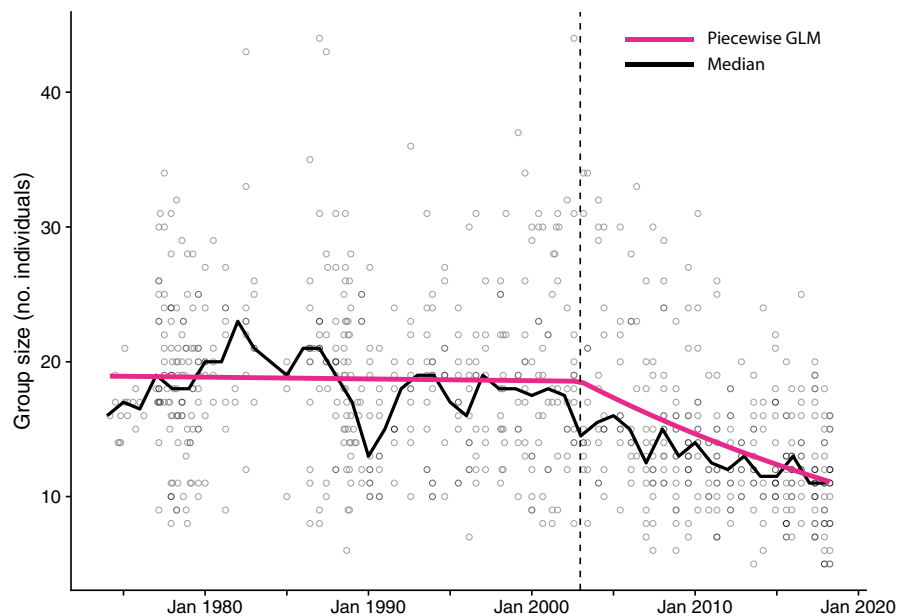
TABLE 2 Statistical fits of piecewise, linear, or intercept-only generalized linear models to howler group census counts and ratios of immatures to adult female and infants to adult female. Comparative model fits were evaluated with ΔAIC scores, where ΔAIC = $AIC_i - AIC_{min}$; i is the model being assessed. ΔAIC scores differing by < 7 are considered to have equal explanatory power. For all models, the independent predictor variable was the year-month date

Response (counts per group)	Model	k	ΔAIC	R^2	Breakpoint	β_1	β_2	p
All individuals	Piecewise	5	0	0.410	2003 ± 1.5	0	−0.033 ± 0.004	<0.001
	Linear	3	63	0.233	-	−0.011 ± 0.001	-	-
	Intercept-only	2	194	-	-	-	-	-
Adult females	Piecewise	5	0	0.150	2002 ± 2.8	0	−0.019 ± 0.004	<0.001
	Linear	3	17	0.078	-	−0.006 ± 0.001	-	-
	Intercept-only	2	56	-	-	-	-	-
Adult males	Piecewise	5	0	0.189	2004 ± 2.0	0.004 ± 0.002	−0.044 ± 0.006	<0.001
	Linear	3	32	0.086	-	−0.008 ± 0.001	-	-
	Intercept-only	2	60	-	-	-	-	-
Juveniles	Piecewise	5	0	0.301	2004 ± 1.1	0.012 ± 0.003	−0.010 ± 0.010	<0.001
	Linear	3	115	0.076	-	−0.012 ± 0.002	-	-
	Intercept-only	2	156	-	-	-	-	-
Infants	Piecewise	5	0	0.367	2002 ± 3.0	−0.013 ± 0.002	−0.024 ± 0.007	<0.01
	Linear	3	9	0.327	-	−0.020 ± 0.001	-	-
	Intercept-only	2	208	-	-	-	-	-
Immatures per female	Piecewise	5	0	0.154	2016 ± 0.8	−0.008 ± 0.001	−0.116 ± 0.060	<0.001
	Linear	3	15	0.08	-	−0.010 ± 0.001	-	-
	Intercept-only	2	135	-	-	-	-	-
Infants per female	Piecewise	5	0	0.168	1977 ± 1.0	0.043 ± 0.030	−0.052 ± 0.030	0.335
	Linear	3	2	0.163	-	−0.008 ± 0.001	-	-
	Intercept-only	2	149	-	-	-	-	-

(1985–2001; 28 censuses) preceding the downturn (12.9 and 9.4 groups, respectively; t = 3.01, df = 54, p = 0.004).

3.2 | Island-wide howler population size

The size of the howler monkey population living on BCI has undergone substantial change since it was first assessed in the early 1930s (Carpenter, 1934). Carpenter (1965) and Milton (1982) summarized the findings of early efforts (1933–1978) to quantify characteristics of the howler monkey population on BCI, including the total number of groups, their average size, and calculated estimates of the number of howlers living on the island. Milton (1996) reported another set of estimates for 1988. Figure 3 shows this published record of population characteristics and extends it with data collected by KM at three additional time points since 1988. We also plot an extrapolated estimate of total population size for 2018.

The number of groups on the island more than doubled between 1933 and 1974, then appeared to plateau at an average of 63 groups (range: 58–70) thereafter (1977–2010). With one notable exception, the average group size remained fairly steady from 1933 to the start of the decline in 2003 that we document here. The one exception was a sharp drop to an average of only 7.9 individuals per group in

1951, which Collias and Southwick (1952) attributed to an epidemic of yellow fever that swept through central Panama in the late 1940s. By the next island-wide group count in 1959, average group size had risen to 18.5 individuals, which was the long-term average value from 1933 to 1997, excluding the data for 1951.

Reflective of these temporal patterns in group number and size, the estimated number of howlers on the island exhibited a net increase of 276% between 1933 and 1977. After 1977, the population appeared to level off, and our new estimates from 1997, 2006, and 2010 are consistent with this trend. Between 1978 and 2010, the island's howler population averaged 1139 individuals (range: 1,069–1,212). Since 2010, group sizes have continued to decline, averaging 10.8 individuals in 2018. If one assumes a current island-wide group count of 68, the average of the two most recent estimates, the total population of howlers on BCI has likely fallen to approximately 734 individuals, a 45.7% decline since its high point in 1977.

3.3 | Decline in fruit resources

Several sets of tree demographic data provide clear evidence of a remarkable island-wide decline in the densities of the large free-standing fig trees, *Ficus yoponensis* and *F. insipida*, species that provide highly
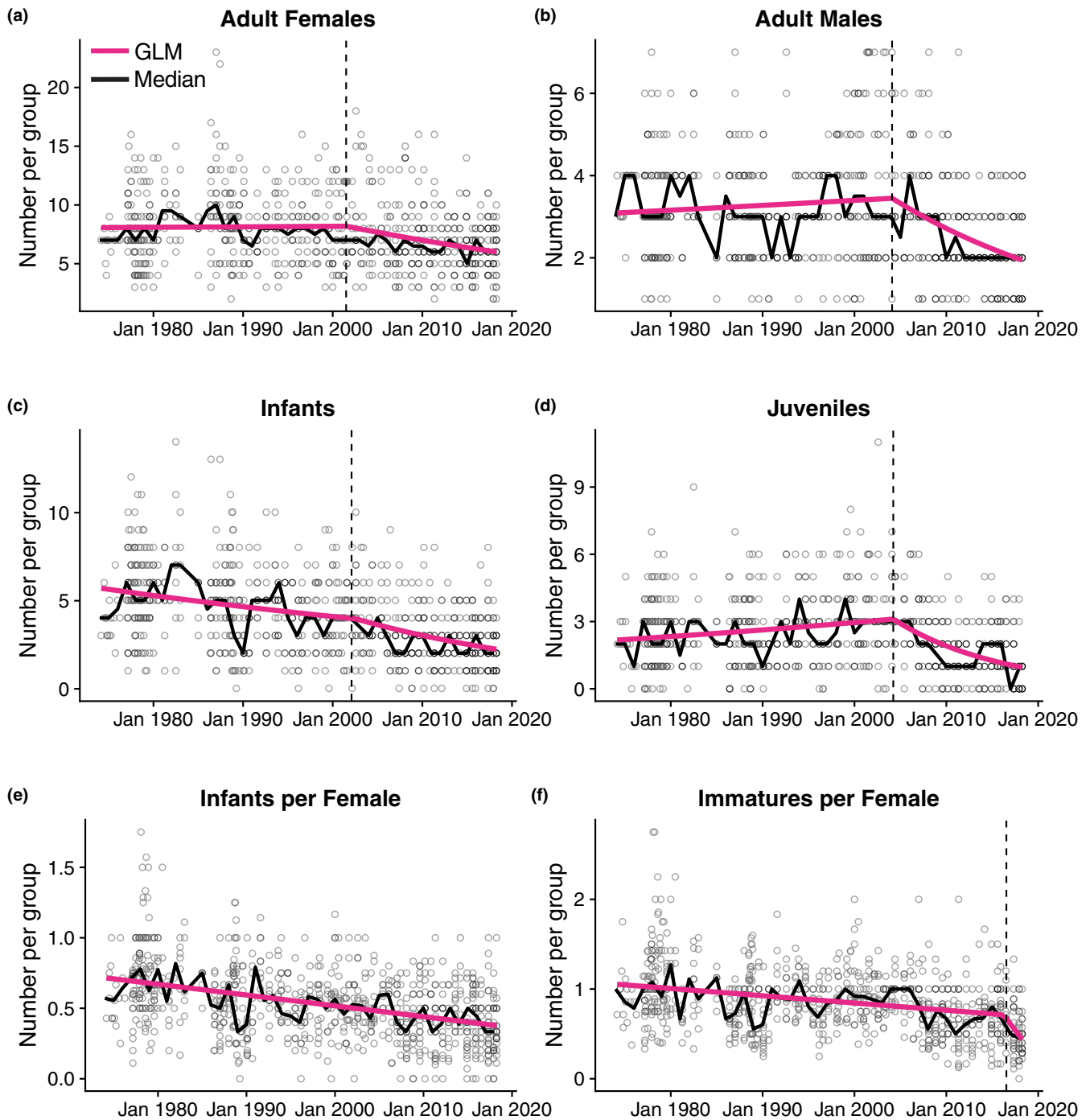
FIGURE 2 Temporal changes in age and gender composition of censused howler groups. Graph layouts as in Figure 1

preferred and heavily used foods for howlers. The 38-year record of fig tree censuses (1973–2011) from the Lutz Catchment shows clear evidence of successional exclusion of *F. yoponensis* and *F. insipida* as the secondary forest areas aged from ~65 years old in 1968 (Knight, 1975) to ~108 years old at the 2011 census. More than 90% of the *F. yoponensis* and 70% of the *F. insipida* died between 1973 and 2011 (Albrecht et al., 2017), and their numbers have continued to decline through 2018 (K. Milton, personal observation). These deaths included 20 individuals (13 *F. insipida* and 7 *F. yoponensis*; mean DBH = 82.4 cm) marked and mapped by KM in 1975, all of

which had died by 2008 (Milton, 1982, unpublished data). Annual rates of fig tree mortality fluctuated considerably between census dates. Over the entire sampling period, the average mortality rate for *F. yoponensis* was roughly twice that for *F. insipida*. Both species suffered accelerated mortality following the strong drought associated with the 1982–83 El Niño, but the former species also suffered particularly high mortality in the early 1990s and again in the early 2000s, while the latter exhibited rising mortality after 2000 (Fig. 4 in Albrecht et al., 2017). As occurred in the Lutz Catchment plot, all the large free-standing figs growing in a 1-ha plot established in 1975 by
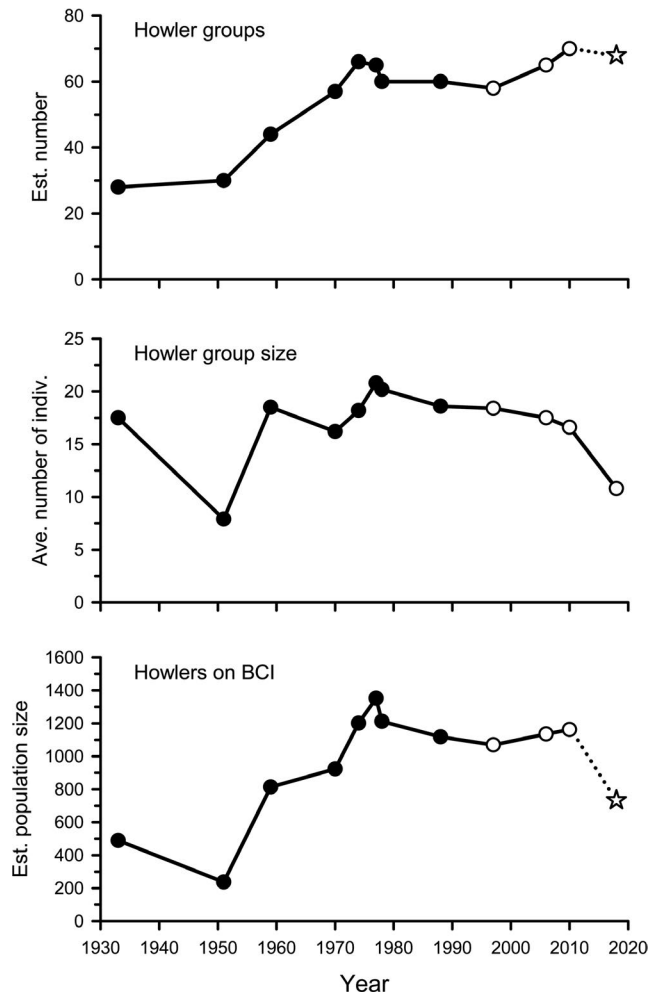
FIGURE 3 Historical and contemporary (this study) estimates of the number of groups, average group size, and total number of howlers living on BCI. The filled symbols are published estimates for 1933 (Carpenter, 1934, 1965), 1951 (Collias & Southwick, 1952), 1959 (Carpenter, 1962, 1965), 1970 (Mittermeier, 1973), 1974, 1977, 1978 (Milton, 1982), and 1988 (Milton, 1996). The open symbols represent unpublished recent estimates based on KM's island-wide groups counts and group censuses made in 1997, 2006, and 2010. The star symbols and dashed lines indicate the estimated number of groups and extrapolated total number of howlers on the island in 2018 (see text)

KM in an area of secondary forest adjacent to the FDP had died by 2008 (Milton, 1982, Plot 1 in Fig. 3.1, p. 29; K. Milton, unpublished data). These included four *F. insipida* and two *F. yoponensis* (mean DBH = 155.5 cm), that had been frequently visited by various howler groups whose home ranges included portions of the old-growth forest characteristic of the FDP. The FDP itself, which was established in relatively old-growth forest, contains very low numbers of these two fig species (combined density of 5–8 trees ≥ 50 cm DBH/50-ha in each 5-year census from 1981/83 to 2015; Hubbell et al., 2015).

Island-wide censuses of the two free-standing fig species confirmed that their successional extirpation has been occurring on the large scale as well. Albrecht et al. (2017) estimate that 70% of the *F. yoponensis* and 61% of the *F. insipida* marked and mapped in the

initial 1985 island-wide census had died by 2011. Remaining trees have continued to die off; as of 2018, there are few large individuals of either species still standing (K. Milton, personal observation). Little evidence of recent recruitment by these two fig species was observed during either the island-wide or Lutz Catchment censuses. In total, only 13 saplings were encountered, and all had recruited in light gaps created by recent treefalls. No saplings were found growing under undisturbed, closed canopy (Albrecht et al., 2017).

Large individuals (≥ 50 cm DBH) of *Brosimum alicastrum* experienced a sharp 21.8% drop in number on the FDP between the first and second plot censuses (1981/1983 to 1985; Figure 4). Following the initial marked decline, numbers have continued to decrease, but much more slowly, averaging 3.9% loss per 5-year census interval. Its dynamics mirror those of numerous tree species in the plot, which experienced high mortality in response to the severe drought conditions associated with a strong El Niño in 1982–83 (Condit, Hubbell & Foster, 1995; Leigh, Windsor, Rand & Foster, 1990). The opposite trend is apparent in the numbers of large *Spondias radlkoferi* trees (≥ 50 cm DBH) in the FDP (Figure 4). While this species is not very common in the plot, its numbers have increased since the first census, with the steepest rise occurring between 1995 and 2000.

4 | DISCUSSION

We will now evaluate evidence regarding demographic processes and species interactions that could have caused the observed decline in howler group size and shifts in age/sex composition on BCI.

4.1 | Emigration or group fission

Neither emigration nor fission appears to explain the observed decline in howler group size. As noted previously, the BCI howler population is essentially closed. While howler monkeys can swim (Froehlich & Thorington, 1982; Gonzalez-Socoloske & Snarr, 2010; Milton, 1982), appreciable emigration of monkeys from the island to adjacent mainland areas has never been observed and would have little to no effect on groups living in the island's interior. Assessing the contribution of group fission to the decline in average group size is more challenging. An increase by 12 in the estimated number of groups living on the island between 1997 and 2010 (Figure 3) suggests that some of the very largest groups (≥ 25 monkeys) may have divided into 2–3 smaller ones, as would be expected under conditions of high intra-group competition for limited food resources (Dittus, 1988). These group splits would have modestly contributed to the drop in average group size, but the frequency of group fission would have had to increase dramatically and across a large number of groups to explain the observed 41.3% drop in average group size between 1997 and 2018. For instance, given the estimated 58 groups living on the island in 1997 and the average group size of 18.4 individuals that year, 41 of the 58 groups (70.7%) would have had to split in half to realize an average group size of 10.8 individuals in 2018. Moreover, this rate of group fission would raise the island
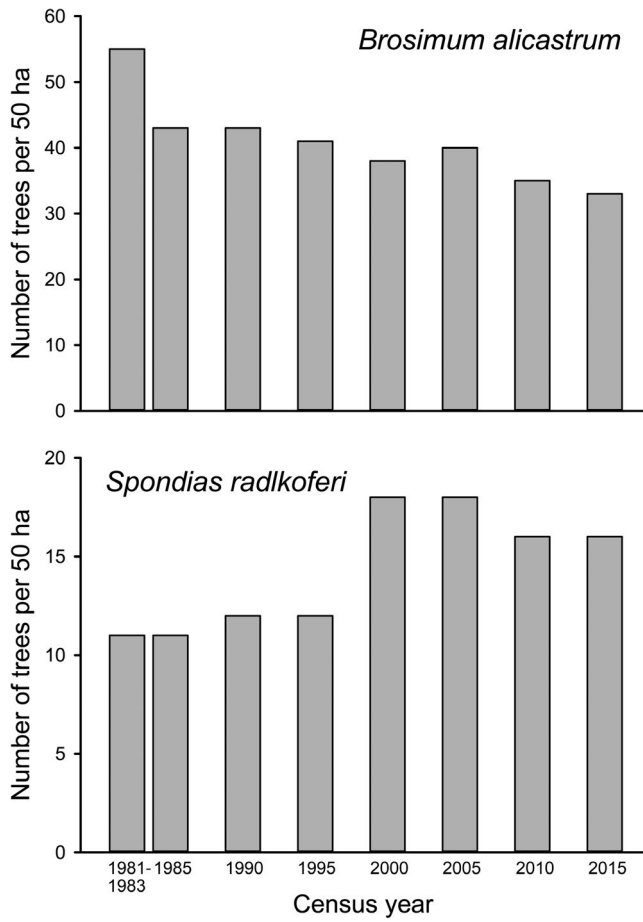
FIGURE 4 Numbers of large (≥ 50 cm DBH) *Brosimum alicastrum* and *Spondias radlkoferi* trees growing in the 50-ha FDP plot on the BCI plateau at 5-year interval from the initial plot census conducted between 1981 and 1983 to the most recent census in 2015. Data were provided by the Center for Tropical Forest Science, Smithsonian Tropical Research Institute (now the Forest Global Earth Observatory, ForestGEO)

group count to 99, which is 29 more than the count of 70 groups estimated in the 2010 island-wide census. Both projections are inconsistent with our observations on group size and number. During neither the annual group composition surveys nor the seven island-wide group counts conducted between 1974 and 2010 did KM observe a substantial number of new, small howler groups appearing within home ranges of groups that she had monitored over several decades. Therefore, while it may occur in particular circumstances, we do not believe group fission is a primary cause of the decline in the sizes of howler groups on BCI.

4.2 | Predation, macroparasites, and disease

Predation on BCI howlers has rarely been observed and never by KM (Milton, 1982, personal observation). Wild harpy eagles (*Harpia harpyja*) were last seen in the Canal Zone almost 70 years ago (Willis & Eisenmann, 1979), but two captive-bred birds were briefly resident on the island between June 1999 and August 2000. They attacked

and fed on a variety of mammals, including 16 howler monkeys (Touchton, Hsu & Palleroni, 2002). Jaguars (*Panthera onca*) are rare in central Panama. Individual cats have occasionally been encountered along BCI trails, with verified sightings in 1983 and 1994 (J. Giacalone & G. Willis, personal communication), along with characteristic claw marks on nearby tree trunks. An extensive footprint and scat survey conducted from 1999 to 2003 (Moreno, Kays & Samudio, 2006) found no evidence of them on BCI during that period. Most recently, a large male jaguar was repeatedly recorded in camera trap photos over a three-month period, from April 20, 2009 to July 20, 2009 (J. Giacalone & G. Willis, personal communication), and may have been responsible for an attack on a subadult male *Cebus capucinus* monkey (Tórrez, Robles, González & Crofoot, 2012).

Puma (*Puma concolor*) regularly occur on the island, where they feed predominantly on collared peccaries (*Pecari tajacu*) and red brocket deer (*Mazama temama*) (Moreno et al., 2006). Samples of puma scat contained no identifiable howler monkey remains, though they occasionally prey upon howlers elsewhere (Chinchilla, 1997). Ocelots (*Leopardus pardalis*) are common on the island and prey mostly on agoutis (*Dasyprocta punctata*) and sloths (*Choloepus hoffmanni and Bradypus variegatus*) (Aliaga-Rossel, Moreno, Kays & Giacalone, 2006; Moreno et al., 2006, J. Giacalone & G. Willis, personal communication). However, they, along with tayra (*Eira barbara*) and large snakes may occasionally prey on immature howlers. During his seminal BCI study, Carpenter (1934, p. 121–122) observed a single unsuccessful attack by an ocelot on a juvenile howler. In general, the impact of these predators on the howler monkey population density and group size appears negligible and cannot explain the observed island-wide decline in average group size.

Howler monkeys are afflicted by a variety of macroparasites, most notably larvae of the bot fly, *Cuterebra baeri*, a species that exclusively infests members of the howler genus, *Alouatta* (Carpenter, 1934; Collias & Southwick, 1952; Milton, 1982, 1996). Milton's (1996) long-term monitoring of bot fly infection rates in the BCI howler population documented annual prevalence ranging from 48 to 76%, with an overall mean infection intensity of 2.8 larvae per monkey. Infection rates peak in the mid-to-late rainy season (Aug.–Nov.). These infestations can be lethal, especially for small infants or any individuals suffering from nutritional stress (low fat reserves and compromised immune responses), a condition that is more common during the mid-to-late rainy season when fruit and young leaves are less available. Bot fly infections are rendered more lethal if accompanied by secondary infections. No discernable increase in the prevalence or intensity of botfly infestation was observed during the annual group censuses conducted over the period of decline in howler group sizes (K. Milton, personal observation).

Epidemics of yellow fever were observed to cause high rates of mortality in Brazilian howler monkey populations in the 1930s and 1940s and have been hypothesized to be responsible for the large drop in howler density on BCI between 1949 and 1951 (Collias & Southwick, 1952). Support for the latter proposition was circumstantial, based on the finding of yellow fever immunity in two of 12 individuals sampled from BCI in 1949, and in larger numbers of

monkeys from eastern and western regions of Panama in 1949–50. Since that time, there have been no reports of confirmed or suspected outbreaks of yellow fever in Panamanian howler monkey populations. Recent epidemics of yellow fever have caused extensive mortality of brown and black howler monkeys (*Alouatta clamitans* and *A. caraya*) in Argentina in 2008 (Agostini et al., 2014; Holzmann et al., 2010; Moreno et al., 2015) and Brazil in 2016 (Tyrrell, 2017).

In summary, while macroparasites and viral disease certainly kill howler monkeys, there is no evidence that rates of mortality on BCI due to parasitism or disease rose precipitously in the early 2000s, prior to, or coincident with, the decline in howler group size. We therefore reject this explanation of the observed demographic shift in howler groups.

4.3 | Decline in fruit resources

The island-wide loss of primary food resources, specifically the loss of almost all the large individuals of *Ficus yoponensis and F. insipida*, is the most parsimonious explanation for the observed reduction in howler group size and shifts in age/size composition. Two episodes of high mortality in free-standing figs in 1992–1994 and 2002–2004 (Fig. 4 in Albrecht et al., 2017) shortly preceded the start of the decline in adult and juvenile howlers in 2002–2004, which has continued to the present. The decline in adult female numbers began several years earlier than that of adult males and juveniles. Female survival may have been more sensitive to the loss of standing fig resources because pregnant and lactating individuals would have had greater nutritional demands and therefore come under greater stress than males or juveniles. The early and continuous decline in the number of infants is consistent with this explanation: food deprivation can suppress secretion of reproductive hormones, ovulation, and estrous cycling, causing reduced fertility (Cameron, 1996; Wade & Schneider, 1992). An undernourished female that does become pregnant may be unable to carry the fetus to term (e.g., Tardif, Ziegler, Power & Layne, 2005), and infants that are born may die due to inadequate production of milk by the mother (Lee, 1987; Lee, Majluf & Gordon, 1991).

It is not surprising that howler demography would be particularly sensitive to changes in the abundance of the two large, free-standing fig trees, *Ficus yoponensis* and *F. insipida*. In addition to providing a preferred and highly nutritious food, these species exhibit a year-round fruiting phenology and large per tree fruit crops (Handley, Gardner & Wilson, 1991; Milton, 1991; Milton, Windsor, Morrison & Estribi, 1982; Morrison, 1978; Wendeln, Runkle & Kalko, 2000). On BCI, these species exhibit two fruiting peaks associated with the dry to wet (April to June) and wet to dry (November to January) season transitions. The latter fruiting peak is particularly critical to howlers since it occurs at a time of year when most other tree species are not producing ripe fruit (Foster, 1982; Milton et al., 1982). Figs have been characterized as a keystone resource in tropical forests because their exploitation by and influence on populations of

frugivorous vertebrates is disproportionately large, relative to their abundance in the forest (Terborgh, 1986).

Our thesis that food limitation caused by the loss of large free-standing fig trees is chiefly responsible for the decline in the average size of howler groups on BCI is further reinforced by the fact that patterns of fluctuation in the abundances of the other preferred fruit tree species, *Brosimum alicastrum* and *Spondias radlkoferi*, do not match changes in the BCI howler population. The El Niño-related drop in the density of large *Brosimum alicastrum* trees followed by a more gradual ongoing decline may have contributed to the reduction in howler group sizes; however, there is no clear correlation between *B. alicastrum* dynamics and specific breakpoints in total group size, adult, or juvenile numbers in the early 2000s. Large *Spondias radlkoferi* trees have actually increased in number, with the greatest increment occurring between 1995 and 2000, just prior to the decline in howler group size. Therefore, no causal link between fluctuations in these species and changes in howler group size or composition is apparent.

The impact of successional extirpation of key large fruit trees is greater than simply the amount of food resources lost. While the deaths of even a few such trees from a howler group's home range can substantially lower overall food availability, it can also disrupt important arboreal travel routes by opening large canopy gaps. Howlers travel only to get to food sources, and these group movements are strongly goal-directed; monkeys travel efficiently along familiar arboreal pathways that serve to connect important food patches in their home range (Garber & Jelinek, 2005; Hopkins, 2011; Milton, 1980). Treefall gaps that form along these well-established travel routes may indirectly raise energy costs by necessitating a longer day range as monkeys must circumvent these open and low canopy areas (Hopkins, 2008; McLean et al., 2016) and climb more to negotiate elevational changes along travel routes and when transferring between disjunct adjacent crowns. If the metabolic costs of travel increase, howlers must expend more energy to acquire sufficient nutrition. This energetic demand would be accentuated for larger groups since the total intake must be higher to satisfy the needs of a greater number of individuals and rates of patch depletion are higher (Chapman & Chapman, 2000). Group cohesion becomes more and more difficult to maintain. We hypothesize that gradual island-wide changes in forest composition and structure over the past 44 years, which included the deaths of nearly all large free-standing fig trees, has caused a reduction in mean group size in the howler population. Reducing mean group size would lower average daily travel distance (lower energy costs) to locate sufficient food for all group members and improve foraging efficiency by reducing the number of monkeys dependent on foods from a declining number of important larger food trees in their home range area.

The situation we describe for the howler monkeys on BCI has been observed or suggested to occur in other forest primate populations. Chapman et al. (2010) analyzed changes in tree species composition and structure over an 18-year period (1989–2006) in a forest compartment characterized as "old-growth" within Kibale

National Park, Uganda. While this stand had experienced little recent disturbance, there was archeological and palynological evidence that it had been heavily disturbed by humans a few hundred years earlier. The study documented a successional decline in density and cumulative DBH of tree species that typically recruit following large-scale disturbances and produce fruits and leaves favored by black-and-white colobus monkeys (*Colobus guereza*). Chapman et al. (2010) hypothesized that this change in forest composition could lead to a reduction in black-and-white colobus monkey populations within this forest compartment, or changes in the monkeys' foraging behavior or diet. However, a recent comprehensive analysis of monkey census records from the park (Chapman et al., 2018) found that black-and-white colobus density changed little between 1970 and 2014 in the "old-growth" stand, ranging from 0.12 to 0.27 groups encountered per km of walked transect; the predicted downward trend in numbers was not apparent. Nevertheless, the average encounter rate (0.20 groups/km) in this mature stand was 2.5 and 3.6 times lower than in the adjacent lightly (0.50 groups/km) or heavily logged (0.71 groups/km) compartments, respectively.

Similarly, the density of spider monkeys (*Ateles geoffroyi*), while quite high in younger secondary forest stands in a Costa Rican lowland wet forest where their favored fruit tree species (*Ficus insipida* and *Spondias mombin*) are abundant, is expected to decline as the forest matures and these key resources become less available (Weghorst, 2007). It is also predicted that species of frugivorous bats that feed heavily on *Ficus spp* within secondary forest on BCI may have suffered the same fate as the howler monkeys (Albrecht et al., 2017; Kalko, Handley & Handley, 1996). In the case of our howler investigation and the studies just mentioned, long-term, regular monitoring efforts were essential to the detection of shifts in forest structure and associated responses in the demography and density of animals that rely on specific plant resources, the availability of which changes as tree species composition shifts over the course of forest succession.

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AUTHOR CONTRIBUTION

DATA AVAILABILITY

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