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REVIEW

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Primate life history, social dynamics, ecology, and conservation: Contributions from long-term research in Área de Conservación Guanacaste, Costa Rica

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Abstract

Research on non-human primates in the endangered tropical dry forest of Sector Santa Rosa (SSR), Área de Conservación Guanacaste (ACG), was launched in 1983 and is now one of the longest running studies of primates globally. Such continuous study provides a rare opportunity to ask questions that are only answerable through decades-long monitoring of these long-lived monkeys. In turn, the mounting data generated by long-term study, including knowledge of lifetime reproductive success, familial relatedness, comprehensive behavioral and dietary repertoires, and patterns of inter- and intra-annual variation in forest productivity, provide diverse opportunities to researchers, and facilitate studies that are of shorter duration. Here, we review some of the contributions of our longitudinal research on white-faced capuchins and Geoffroy's spider monkeys, together with newer studies on mantled howler monkeys. We begin by synthesizing findings from our research on demography, dispersal, social relationships, and reproduction. These life history and social traits interact with their

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foraging and sensory ecology, which we review next. We end by highlighting how the longitudinal study of primates in Sector Santa Rosa has made direct and indirect contributions to the conservation of the critically endangered dry forest biome and its inhabitants, as well as to education, community, and forest restoration initiatives. In particular, we focus our review on how long-term research is uniquely positioned to make key contributions spanning different topical areas.

Abstract in Spanish is available with online material.

KEYWORDS

life histories, longitudinal research, plant–animal interactions, reproductive strategies, sensory ecology, social relationships

1 | INTRODUCTION

Primates and other long-lived mammals exhibit slow life histories and low population densities. Accordingly, field biologists studying these species are typically plagued with small sample sizes that limit power for addressing questions related to fitness, variation, and adaptation. Additionally, primate habitats often show seasonal and inter-annual variation, making it difficult to use short-term studies to understand their ecology and adaptive complexes (Chapman et al., 2017). Only through longitudinal study of tens to hundreds of animals are we able to begin to answer key questions about animal social systems and relationships, ecological niches, and behavioral plasticity, and to measure the fitness consequences of individual variation (Schradin & Hayes, 2017). Field primatology in Sector Santa Rosa (SSR), Área de Conservación Guanacaste (ACG), has been ongoing since its inception in 1983 by Linda Fedigan, making this project one of the longest running continuous studies of primates globally (Kappeler et al., 2012). Over the past 37 years of study in this tropical dry forest, much has been learned about its three resident species of primates: white-faced capuchins (*Cebus imitator*), Geoffroy's spider monkeys (*Ateles geoffroyi*), and mantled howler monkeys (*Alouatta paliatta*; Figure 1). Here, we review key advances in our understanding of the demography, life history, dispersal patterns, social relationships, reproduction, diet, sensory ecology, and conservation of the SSR primates that have been directly enabled by longitudinal research. Our review focuses primarily on the capuchin and spider monkeys, which we have intensively studied for decades. Only one group of spider monkeys has been studied at SSR given their large home range. To combine data from multiple groups and make our review more comprehensive, we include findings on spider monkeys from Punta Laguna, our team's other field site in the Yucatan peninsula, Mexico, which is the longest running project on spider monkeys (Ramos-Fernández et al., 2018). Further, we include details of howler monkey foraging ecology and demography, which have also been investigated, although not continuously, in SSR. We end by highlighting how our research has contributed to current conservation and education initiatives, and how the knowledge gained will promote the future protection of these iconic mammals.

2 | DEMOGRAPHY AND LIFE HISTORIES

Evolutionary biologists seek to quantify life-history variables in order to model population dynamics and to understand

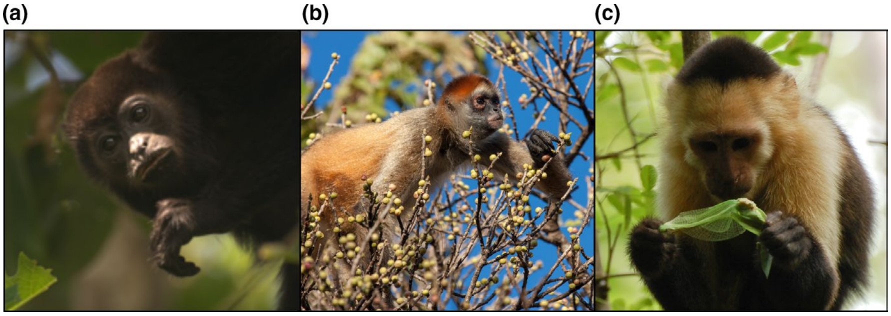


FIGURE 1 Three primate species live sympatrically in the tropical dry forests of Sector Santa Rosa, Área de Conservación Guanacaste: (a) folivorous–frugivorous mantled howler monkey (*Alouatta paliatta*), (b) frugivorous Geoffroy's spider monkey (*Ateles geoffroyi*), and (c) omnivorous white-faced capuchin (*Cebus imitator*). Howler and capuchin monkeys live in cohesive social groups, whereas spider monkey groups are fluid with the formation of subgroups highly variable in size and composition. These species overlap in the fruits they consume, but also show considerable divergence, with capuchins eating the widest range of plant species. Photo credit: Amanda Melin (a, c), Fernando Campos (b)

TABLE 1 Basic biological and life history variables for ACG primates

	Ateles geoffroyi	*Alouatta palliata*	*Cebus imitator*	References/notes
Adult weight (♂/♀)	♂: 8.375 kg ♀: 6.624 kg	♂: 6.528 kg ♀: 4.02 kg	♂: 3.333 kg ♀: 2.283 kg	Glander et al. (1991)[a]
Adult length (♂/♀)	♂: 1,227 mm (body 466 + tail 761) ♀: 1,148 mm (body 425 + tail 723)	♂: 1,111 mm (body 479 + tail 632) ♀: 1,070 mm (body 455 + tail 615)	♂: 843 mm (body 372 + tail 471) ♀: 809 mm (body 365 + tail 444)	Glander et al. (1991)[a]
Brain volume (endocranial volume)	♂: 101 cc ♀: 110 cc	♂: 52 cc ♀: 48 cc	♂: 74 cc ♀: 72 cc	Isler et al. (2008)[a]
Dietary category[b]	Frugivore	Folivore–frugivore	Omnivore	Terborgh (1983)[a]
♀ age at first birth	7.1 years	3.5 years	median 6.70 years, *SD* = 0.7, *N* = 42;	Di Fiore et al. (2010)[a], Glander (1980)[a], Fedigan unpublished data
Interbirth interval	34.7 months	19.9–22.5 months	26.4 months	Di Fiore et al. (2010)[a], Glander (1980)[a], Fedigan and Rose (1995), Fedigan et al. (2008)
Gestation	~7.5–7.7 months	~6.2 months	5.5 months	Di Fiore et al. (2010)[a], Carnegie et al. (2011)
Weaning age	19–31 months	~12 months	14–23 months	Di Fiore et al. (2010)[a], Sargeant et al. (2015)
♀ max life span (wild/captive)	47 years (captive) conservatively estimated at 35 years (wild)	20 years (captive) 15 years (wild)	unknown (captive) 37 years (wild)	Hakeem et al. (1996), Fragaszy et al. (2004), Fedigan et al. (2008), Di Fiore et al. (2010) https://genomics.senescence.info/species/entry.php?species=Ateles_geoffroyi https://genomics.senescence.info/species/entry.php?species=Alouatta_palliata Aureli & Schaffner, unpublished data
♂ puberty	4–5 years (earliest behavioral correlates of maturity)	Pubertal growth spurt at 3–5 years; sexual maturity at 3.5 years	6 years	Glander (1980)[a], Froehlich et al. (1981)[a], Di Fiore et al. (2010)[a], Jack et al. (2014), Aureli & Schaffner unpublished data
♂ age at adult size/Maturity	Adult body size at 8 years	3.5–5 years	10 years, but does not attain full suite of secondary sex traits unless alpha status is attained	Fedigan and Jack (2004), Di Fiore et al. (2010)[a], Aureli & Schaffner unpublished data
♂ max life span (wild/captive)	40+ years (captive) 20 years (wild)	Unknown (captive) 16.6 years (wild)	54 years (captive) >25 years (wild)	Di Fiore et al. (2010)[a], Crilly (2017)[a] Weigl (2005)[a] Aureli & Schaffner unpublished data, Jack & Fedigan unpublished data
Age at dispersal	♀: mean 5.5 years, range 4.9–6.3 (based on age of disappearance from natal group)	♂: mean 2.5 years; range 1.5–5.5 years ♀: mean 2.6 years; range 1.5–6.5 years	♂: 4.5 years (5.5. for confirmed dispersers only); range 20 months to 11 years	Jack and Fedigan (2004a), Clarke and Glander (2008)[a], Vick (2008)[a], Jack et al., 2012
Secondary dispersal (yes/no)	♀: Typically, no	♂ ♀: Yes; at a mean age of 10 years	♂: Yes; males change groups approximately every 4 years	Shimooka et al. (2008)[a], Clarke and Glander (2010)[a], Jack and Fedigan (2004b)

[a] Indicates a source that is not based on the SSR primate populations. In these cases, we have selected sources that come from populations as close to SSR as possible.

[b] See Table 2 for a detailed breakdown of plant species consumed.

life-history evolution (Oli & Dobson, 2003). Overall, primates are characterized by their long life spans and slow life histories (Kappeler & Pereira, 2003), yet there is wide variation in the order. For example, gray mouse lemurs (*Microcebus murinus*) typically live 8–12 years (Languille et al., 2012). While this is triple the life span of a mouse (3–4 years; (Strong et al., 2008), it is comparatively short for a primate. Free-ranging but provisioned macaques (*Macaca fuscata*, *Macaca mulatta*) can live into their early 30s, and great apes in the wild may live more than 40–50 years (*Pan troglodytes* 63 years, *Pongo abelii* 53 years, *Gorilla gorilla beringei* 44 years, (Fedigan & Pavelka, 2011)). Given their body sizes (weight range for capuchins is 3–4 kg and for spider monkeys is 6–9 kg, Table 1), these monkeys are remarkably long-lived. Capuchins and spider monkeys have both been documented to live to >45 years in captivity and estimated to live into their late 30s in the wild (Crilly, 2017; Di Fiore et al., 2010; Perry, 2012). However, to understand the evolution of life history traits such as life span, data from wild populations are essential. However, most data on primate life spans are derived from captive populations, as many primates simply live longer than the duration of most research programs (but see Bronikowski et al., 2002, 2011; Colchero et al., 2016; Wood et al., 2017). Here is a clear area where long-term field research in which known individuals are tracked from birth to death is well-positioned to contribute valuable data on important life-history traits, including life expectancy and life span under natural conditions.

The capuchins at SSR represent one of very few wild primate populations for which enough individual-based long-term demographic data have been collected to study natural processes of senescence and aging in the wild (Strier et al., 2010). Life tables constructed from demographic data based on capuchins in Santa Rosa have enabled us to characterize age- and sex-specific trajectories of mortality in capuchins. By placing them in comparative context with other primates for which longitudinal data are available, we have been able to illuminate the evolutionary landscape of primate aging (Bronikowski et al., 2016). These efforts have revealed ways in which human aging lies on a continuum with that of other primates (Bronikowski et al., 2011; Colchero et al., 2016), as well as ways in which humans are distinct. For example, mid-life female reproductive senescence—a universal phenomenon across human populations—does not occur in capuchins or in other wild non-human primates (Alberts et al., 2013). Such insights are only made possible by cross-species comparisons of long-term life history data from multiple primate populations. In SSR, the presence of three closely related, sympatric, and continuously monitored primate species with different paces of life invites a future research program on comparative biological processes and behavioral dynamics during aging.

Thirty-four years of data on reproductive and mortality rates of individuals tracked longitudinally have allowed us to quantify their life-history parameters in this habitat and to begin assessing the adaptive significance of different phenotypes. Among the three species of primates in SSR, we find that spider monkeys have the oldest median age at first birth (7.1 years; Di Fiore et al., 2010), followed by capuchins (6.7 years; Fedigan unpublished data) and howlers (3.5 years, Glander, 1980). Gestation length, age at weaning, and interbirth intervals follow this same pattern, with spider monkeys showing the longest periods for each of these variables, and howlers the shortest (Table 1).

Intriguingly, male life histories do not follow the same general pattern across the three sympatric species in SSR. For example, capuchin males take much longer to attain full adult body size (10 years) in comparison to the larger spider (8 years) and howler monkeys (5 years). Though male capuchins are capable of reproduction around age 7, most do not reproduce prior to attaining full adult body size (Jack et al., 2014; Perry, 2012). We hypothesize that the prolonged subadult phase experienced by capuchin males is adaptive, for example, if delaying physical maturity enables males to move more easily between social groups during dispersal events (Jack, 2003a, see also Perry et al., 2017). A remarkable discovery, revealed only after many years of study, was the existence of male dimorphism in capuchins (Jack & Fedigan, 2018; Jack et al., 2014). While we observed from the beginning of our studies that alpha male capuchins were consistently the largest males in a social group, we initially predicted that they achieved alpha status due to their large size and increased competitive ability. However, only after collecting years of long-term behavioral data on males through multiple dispersal events, and combining these data with multi-year non-invasive fecal hormone sampling, did it become clear that alpha males exhibit a distinct phenotype in both appearance and behavior, which emerged once they (or as they) became the most dominant male. Though both *types* of males are reproductively viable (i.e., able to sire offspring), alphas maintain significantly higher androgen levels than subordinate adult males (Jack et al., 2014; Schoof et al., 2011). This phenomenon is similar to (though far more subtle than) the pattern of alternative male morphologies observed in mandrills (Setchell & Dixson, 2001) and orangutans (Dunkel et al., 2013). There is some indication that spider monkeys also delay the full expression of some secondary sex traits, such as the orange coloration around a sternal gland, which appears only on some males and females (Aureli & Schaffner, unpublished data). Further study, including the collection of additional behavioral, morphological, and endocrinological data on both spider and howler monkeys, will aid in our ability to compare and contrast patterns of interspecific differences in male life-history traits and their evolution.

3 | DISPERSAL PATTERNS

Among group-living mammals, one or both sexes typically disperse from their natal groups, which is favoured by natural and kin selection as it decreases inbreeding and the deleterious consequences of mating with close kin, and can facilitate kin cooperation or reduce kin competition (Lukas & Clutton-Brock, 2011; Pusey & Packer, 1987; West et al., 2002). Importantly, dispersal patterns have far-reaching consequences for the quality and quantity of social relationships of individuals within and between groups, as well as the nature of mate choice and inter- and intrasexual competition (ibid). Patterns of male and female dispersal patterns are hypothesized to be influenced by the distribution and defensibility of food resources, as well as by phylogenetic inertia (i.e., a species evolving from a species with male-biased dispersal tends to retain this pattern unless the new environment favors a different pattern). This topic has received

TABLE 2 Plant species and parts observed to be consumed by capuchin, howler, and spider monkeys Sector Santa Rosa, Área de Conservación Guanacaste, Costa Rica

		FRUIT			**LEAVES**			**FLOWERS**		
Family	**Species**	**Capuchin**	**Howler**	**Spider**	**Capuchin**	**Howler**	**Spider**	**Capuchin**	**Howler**	**Spider**
Anacardiaceae	*Astronium graveolens*					🟥	🟫		🟥	
	Spondias mombin	🟦		🟫		🟥			🟥	🟫
	Spondias purpurea	🟦	🟥	🟫		🟥				
	Spondias radlkoferi	🟦		🟫		🟥				
Annonaceae	*Annona holosericea*	🟦								
	Annona purpurea	🟦		🟫				🟦		
	Annona reticulata	🟦		🟫			🟫	🟦		🟫
	Desmopsis bibracteata	🟦								
	Sapranthus palanga	🟦						🟦		🟫
Apocynaceae	*Forsteronia spicata*	🟦				🟥	🟫			
	Gonolobus barbatus	🟦								
	Prestonia riverae	🟦								
	Stemmadenia pubescens	🟦		🟫						
Araceae	*Syngonium angustatum*	🟦					🟫			
Araliaceae	*Aralia excelsa*	🟦	🟥	🟫		🟥				
Arecaceae	*Acrocomia aculeata*	🟦								
	Bactris guineensis	🟦								
Asclepiadaceae	*Blepharodon mucronatum*	🟦								
	Matelea quirosii	🟦								
	Marsdenia engleriana			🟫			🟫			
Bignoniaceae	*Amphilophium crucigerum*	🟦								
	Amphilophium paniculatum	🟦								
	Callichlamys latifolia	🟦								
	Ceratophytum tetragonolobum	🟦								
	Handroanthus ochracea	🟦				🟥			🟥	🟫
	Pseudobombax septenatum		🟥	🟫						🟫
	Tabebuia rosea		🟥			🟥			🟥	
Boraginaceae	*Cordia alliodora*					🟥			🟥	
	Cordia guanacastensis	🟦						🟦		
	Cordia panamensis	🟦		🟫		🟥	🟫			
Bromeliaceae	*Bromelia karatas*	🟦								

References: Aureli, Schaffner and Murillo-Chacon (unpublished data), Melin, Webb, and Cheves Hernandez (unpublished data), Zandona (unpublished data), Hogan et al. (2016), Melin et al. (2012), Melin, et al. (2014)), Welker (2004), Larose (1996), Morera-Avila (1996).

Note that howler monkeys have been studied least intensively in ACG and their dietary repertoire might not be fully represented relative to the other two species.

	Bromelia pinguin	🟦		🟫						
Burseraceae	*Bursera simaruba*	🟦	🟥	🟫		🟥	🟫		🟥	🟫
	Bursera tormentosa	🟦								
Cactaceae	*Hylocereus costaricensis*	🟦								
Capparidaceae	*Capparis indica*	🟦				🟥				
Celastraceae	*Maytenus segoviarum*	🟦								
	Semialarium mexicanum	🟦				🟥				
Chrysobalanaceae	*Hirtella racemosa*	🟦								
	Licania arborea		🟥			🟥		🟦	🟥	
Clusiacea	*Garcinia intermedia*			🟫						
Cochlospermaceae	*Cochlospermum vitifolium*					🟥			🟥	🟫
Combretaceae	*Combretum farinosum*							🟦		
	Terminalia spp.					🟥				
Cyperaceae	*Cyperus luzulae*	🟦								
Dilleniaceae	*Curatella americana*	🟦						🟦		
	Davilla kunthii	🟦								
	Doliocarpus dentatus	🟦		🟫						
Ebenaceae	*Diospyros salicifolia*	🟦		🟫						
Elaeocarpaceae	*Sloanea terniflora*	🟦		🟫		🟥				
Erythroxylaceae	*Erythroxylum havanense*	🟦								
Euphorbiaceae	*Manihot aesculifolia*	🟦								
	Mabea occidentalis									
	Margaritaria nobilis	🟦								
	Sapium glandulosum	🟦		🟫		🟥				
	Sapium macrocarpum	🟦				🟥			🟥	
	Sebastiania pavoniana	🟦								
Fabaceae	*Albizia adinocephala*		🟥			🟥			🟥	
	Albizia saman	🟦	🟥	🟫		🟥	🟫		🟥	
	Andira inermis					🟥				
	Bauhinia ungulata							🟦		
	Cassia grandis							🟦		
	Centrosema macrocarpum							🟦		
	Dalbergia retusa					🟥				
	Diphysa americana	🟦		🟫			🟫			🟫
	Enterolobium cyclocarpum		🟥			🟥			🟥	
	Gliricidia sepium	🟦				🟥			🟥	
	Hymenaea courbaril					🟥	🟫	🟦	🟥	🟫
	Inga vera	🟦		🟫		🟥			🟥	
	Lonchocarpus costaricensis		🟥			🟥			🟥	
	Lonchocarpus minimiforus					🟥				

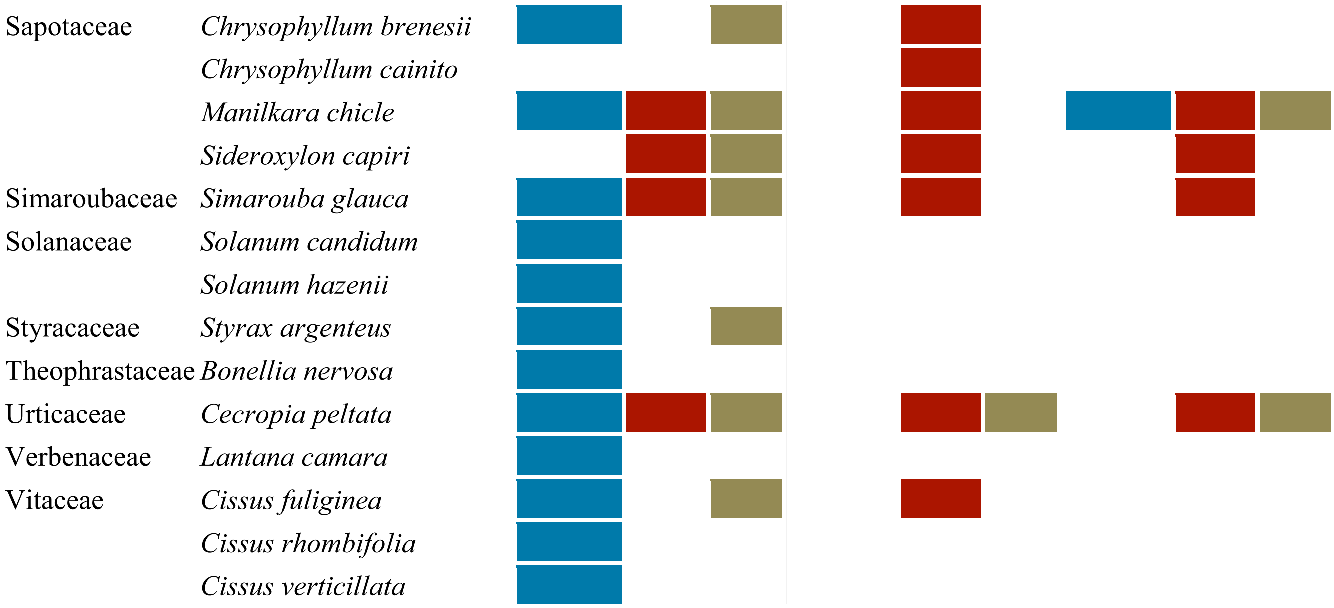
(Continued)

	Lysiloma divaricatum					🟥				🟫
	Machaerium biovulatum					🟥				
	Quercus oleoides	🟦		🟫						
	Swartzia cubensis	🟦	🟥	🟫						
	Vachellia collinsii	🟦		🟫				🟦		
	Vachellia cornigera	🟦								
Lauraceae	*Ocotea veraguensis*	🟦		🟫			🟫			
Malpighiaceae	*Bunchosia polystachia*	🟦		🟫						
	Byrsonima crassifolia	🟦		🟫						
	Malpighia glabra	🟦								
Malvaceae	*Apeiba tibourbou*	🟦		🟫		🟥	🟫			
	Guazuma ulmifolia	🟦	🟥	🟫		🟥				
	Luehea candida	🟦		🟫		🟥		🟦	🟥	🟫
	Luehea speciosa	🟦		🟫		🟥		🟦	🟥	🟫
	Malvaviscus arboreus	🟦						🟦		
	Pochota fendleri			🟫		🟥			🟥	🟫
	Sida latifolia	🟦								
	Sterculia apetala	🟦		🟫		🟥				
Melastomataceae	*Miconia argentea*	🟦								
	Mouriri myrtilloides	🟦		🟫						
Meliaceae	*Cedrela odorata*	🟦								
	Swietenia macrophylla	🟦								
	Trichilia americana	🟦		🟫						
	Trichilia glabra	🟦								
	Trichilia havenensis	🟦								
	Trichilia martiana	🟦		🟫		🟥				
	Trichilia trifolia	🟦				🟥				
Mimosaceae	*Lysiloma auritum*					🟥			🟥	
Moraceae	*Brosimum alicastrum*	🟦		🟫		🟥	🟫		🟥	
	Castilla elastica	🟦		🟫		🟥				
	Ficus bullenei	🟦		🟫						
	Ficus citrifolia	🟦		🟫						
	Ficus cotinifolia	🟦	🟥	🟫		🟥	🟫			
	Ficus goldmanii	🟦	🟥	🟫		🟥	🟫			
	Ficus hondurensis	🟦	🟥	🟫		🟥	🟫			
	Ficus morazaniana	🟦		🟫						
	Ficus obtusifolia	🟦		🟫						
	Ficus ovalis	🟦	🟥	🟫		🟥				
	Maclura tinctoria	🟦	🟥	🟫		🟥			🟥	
	Trophis racemosa	🟦								
Muntingiaceae	*Muntingia calabura*	🟦		🟫		🟥			🟥	

(Continued)

Musaceae	*Musa acuminata*	🟦		🟫						
Myrtaceae	*Eugenia acapulcensis*			🟫						
	Eugenia salamensis	🟦		🟫						
	Psidium guajava	🟦								
Nyctaginaceae	*Pisonia macrantocarpa*	🟦								
Olacaceae	*Ximenia americana*	🟦	🟥							
Orchidaceae	*Brassavola nodosa*				🟦					
Papilionaceae	*Acosium panamense*					🟥				
Passifloraceae	*Passiflora platyloba*	🟦		🟫						
	Passiflora vitifolia	🟦		🟫						
Poaceae	*Lasiacis nigra*	🟦								
	Lasiacis sorgnoidea	🟦								
	Streptochaeta spicata	🟦								
Polygonaceae	*Coccoloba guanacastensis*	🟦		🟫						
Primulaceae	*Ardisia revoluta*	🟦				🟥				
Rhamnaceae	*Karwinskia calderonii*	🟦	🟥	🟫						
	Krugiodendron ferreum	🟦		🟫						
Rubiaceae	*Alibertia edulis*	🟦		🟫						
	Calycophyllum candidissimum			🟫		🟥	🟫	🟦		
	Chomelia spinosa	🟦		🟫		🟥				
	Exostema mexicanum	🟦				🟥			🟥	
	Genipa americana	🟦		🟫	🟦					
	Guettarda macrosperma	🟦		🟫		🟥			🟥	
	Hamelia patens	🟦								
	Ixora floribuna	🟦		🟫						
	Randia monantha	🟦		🟫						
	Randia thurberi	🟦								
Rutaceae	*Citrus aurantifolia*	🟦								
	Zanthoxylum setulosum	🟦								
Salicaceae	*Casearia arguta*	🟦		🟫						
	Casearia nitida	🟦								
	Casearia sylvestris	🟦								
	Prockia crucis	🟦		🟫						
	Xylosma flexuosa	🟦								
	Zuelania guidonia	🟦		🟫		🟥				
Santhalaceae	*Phoradendron quadrangulare*	🟦				🟥	🟫			
	Phoradendron racemosum			🟫			🟫			
Sapindaceae	*Allophylus racemosus*	🟦		🟫						
	Cupania guatemalensis					🟥				
	Dilodendron costaricense	🟦	🟥	🟫						
	Thouinidium decandrum					🟥				

(Continued)



Sapotaceae	*Chrysophyllum brenesii*	🟦		🟫		🟥				
	Chrysophyllum cainito					🟥				
	Manilkara chicle	🟦	🟥	🟫		🟥		🟦	🟥	🟫
	Sideroxylon capiri		🟥	🟫		🟥			🟥	
Simaroubaceae	*Simarouba glauca*	🟦	🟥	🟫		🟥			🟥	
Solanaceae	*Solanum candidum*	🟦								
	Solanum hazenii	🟦								
Styracaceae	*Styrax argenteus*	🟦		🟫						
Theophrastaceae	*Bonellia nervosa*	🟦								
Urticaceae	*Cecropia peltata*	🟦	🟥	🟫		🟥	🟫		🟥	🟫
Verbenaceae	*Lantana camara*	🟦								
Vitaceae	*Cissus fuliginea*	🟦		🟫		🟥				
	Cissus rhombifolia	🟦								
	Cissus verticillata	🟦								

extensive attention in primatology (Clutton-Brock & Janson, 2012; Kappeler & Pereira, 2003; Pusey & Packer, 1987). An thorough review of these topics is beyond the scope of this manuscript, but long-term studies make important contributions of data that inform evolutionary theory about group residency patterns, competition landscapes, and mechanisms of sexual selection. This includes data on: (a) *dispersal patterns* and the extent to which these are flexible; (b) *nature of social relationships* among and between group members, and sources of variation; (c) the *fitness landscapes*, that is, patterns of reproductive success and skew, including patterns of mortality, not only as a snapshot in time (e.g., offspring sired in a group during a small window in time), but also across the reproductive lifetimes of individuals. Below, we highlight examples of these contributions from our research at Santa Rosa.

While short-term studies of a few years may be sufficient to document which sex(es) typically disperse, we have learned from longer studies that dispersal patterns can be far more variable than initially believed. Each of the three primates in SSR displays a different "typical" dispersal pattern: howler monkeys show male dispersal and at least some female dispersal, spider monkeys tend toward female dispersal and male philopatry, and capuchins are male-dispersed and female philopatric. These divergent dispersal patterns, accompanied by the differing diets of the three species, provide an exceptional natural experiment for investigating the selective pressures driving these differences, and their consequences, within the same habitat.

The male-biased dispersal pattern found in capuchins is shared with Cercopithecinae, a prominent radiation of African and Asian monkeys, including the baboons (*Papio* spp.) and macaques (*Macaca* spp.), although not without exception (e.g., Guinea baboons, Kopp et al., 2015). Male white-faced capuchins typically disperse from their natal group prior to attaining sexual maturity and continue to disperse throughout their lives (Jack & Fedigan, 2004a; Jack et al., 2012). Our analysis of residency patterns for 61 immigrant males in five study groups over a total of 38 observation years found that males disperse on average every 3.4 years, and group residency lengths ranged 4–67 months (Jack & Fedigan, 2004b). By analyzing relatedness through genotyping fecal DNA, combined with all-occurrences' records of group movement over 20 years, we have shown that many males emigrate in parallel with other males, often continue to reside with close male kin in their breeding group, and have opportunities to form long social relationships with these related males (Wikberg et al., 2014, 2018). Males dispersing from their natal group often do so with similar-aged paternal half-siblings (Wikberg et al., 2018), and capuchin males join groups containing familiar males more often than expected by chance (Jack, 2003b, Jack & Fedigan, 2004b, see similar findings from the nearby study site of Lomas Barbudal in Perry, 2012). While this pattern of parallel dispersal from the natal group is common in many male dispersed primates, the practice usually wanes during secondary dispersal events when males move between breeding groups (Jack, 2003a). Similar to dispersal patterns reported for male lions, male capuchins continue to disperse in parallel throughout their lives thereby enabling the maintenance of coalitionary partners that are crucial for gaining access to a social group (Jack & Fedigan, 2004b; Packer & Pusey, 1997).

The female-biased dispersal pattern observed in spider monkeys closely parallels chimpanzee dispersal and thus represents an interesting case of socioecological convergence among two distantly related taxa. Studies of spider monkeys at multiple sites have now documented that some females do not emigrate and instead reproduce in their natal group, indicating that, similar to chimpanzees, this pattern of female-biased dispersal can be flexible under some conditions (Shimooka et al., 2008; Walker & Pusey, 2020). Genetic data indicate that some breeding female spider monkeys are immigrants while others are natal (Wikberg, unpublished data), which corresponds to observations of the SSR study group. All but one of the natal females that reached sexual maturity ($N = 14$) disappeared when they reached emigration age (Table 1). The female that remained reproduced in the natal group when she was 8 years old. A few similar cases have occurred among spider monkeys at Punta Laguna, Mexico (Vick, 2008). We have not witnessed parallel dispersal, and it is unclear whether secondary dispersal occurs among spider monkey females as we have not observed any cases of adult female immigration (i.e., females with offspring) at SSR, though some cases have been observed at Punta Laguna (Vick, 2008). In study sites where monkeys of multiple groups were individually recognized, females did not immigrate from neighboring groups (Shimooka et al., 2008), indicating they travel considerable distances to find a new group.

In addition to the insights gained by characterizing the most common dispersal pattern within each study species, cases of dispersal by the more philoptaric sex have important implications for the costs and benefits of dispersal as well as each species' capacity for behavioral flexibility (Clutton-Brock & Lukas, 2012; Lukas & Clutton-Brock, 2011; Walker & Pusey, 2020). Understanding the conditions under which these cases occur, as well as their frequency, can also help us interpret data on patterns of genetic diversity in these species. Between 1986 and 2007, we documented five cases of female capuchins immigrating into our study groups, often in association with alpha male replacements (Jack & Fedigan, 2009). Only one of these immigrant females remained in her new group for several years (6.7 years, Jack & Fedigan, 2009), and genetic analysis demonstrated that she had the same mtDNA haplotype as the natal females, possibly indicating that she dispersed between relatively recent fission products (Wikberg, unpublished data). Evidence from the study of group fissions among capuchins, which have occurred twice in our study history, suggests such a scenario is possible. In both occurrences, the split occurred along matrilines and at group sizes over 30 monkeys. Genetic analyses also revealed an additional case of female immigration, and this female remained in the group until old age (Wikberg unpublished data).

Among the SSR spider monkeys, when the number of adult males in the group is high relative to the number of adult females, maturing males can be ostracized and the potential for lethal aggression, or the peripheralization of younger males, can result in male dispersal and immigration to other groups (Aureli et al., 2013). We have also witnessed two cases of immigration by multiple males and the subsequent disappearance of resident males during our 17 years of study (Aureli et al., 2013). Contrary to what would be expected if males were invariably philopatric, analysis of nuclear DNA of all group members indicates that the males were no more closely related to one another than were group females (Aureli et al., 2013), nor does our analysis of mitochondrial DNA find any evidence of sex-biased dispersal (Wikberg unpublished data). These data establish that it is possible for the typically resident sex to disperse and successfully establish themselves as long-term residents in their new group, highlighting the plasticity of dispersal patterns that can only be revealed through long-term study. Evidence of male dispersal has also been found among white-bellied spider monkeys (*Ateles belzebuth*, Di Fiore et al., 2009), as well as in chimpanzees (Sugiyama, 2004), which converge on numerous aspects of spider monkey sociality, including male philopatry and a high degree of fission–fusion dynamics (Sugiyama, 1999). Overall, there seems to be greater flexibility in dispersal patterns among spider monkeys than capuchins, and our long-term research has provided important data about the demographic circumstances leading to these rare events, but much work remains to be done.

4 | SOCIAL RELATIONSHIPS

Group-living primates form enduring relationships with others throughout the course of their long lives. Due to the considerable variation in the form, strength, and nature of social relationships, comparative studies among primates can be used to ask questions about the costs and benefits, and, ultimately, the evolution of social bonds (Isbell, 2004; Shultz et al., 2011; Sterck et al., 1997; Wrangham, 1980). By combining the intensive and repeated observations needed to study the social patterns of primates with detailed demographic data and non-invasive sampling to estimate body condition, physiological state, and exposure to pathogens, biologists can examine how social relationships affect fecundity, health, and survival. Such studies provide key insights into the costs and benefits of sociality and allow us to study its evolution (Ostner & Schülke, 2018; Snyder-Mackler et al., 2020; Thompson, 2019).

Patterns of dispersal are predicted to be tightly linked to strength of social bonds (West et al., 2002; Wrangham, 1980; Sterck et al., 1997, p. 19), and empirical studies often (but not always) document a kin bias in affiliation (Archie et al., 2006; Carter et al., 2013; Di Fiore & Fleischer, 2005; Gompper et al., 1997; Griffin & West, 2003; Guilhem et al., 2000; Hirsch et al., 2012; Kapsalis, 2004; Möller, 2012; Wahaj et al., 2004; Wikberg et al., 2012, 2014; Wilkinson, 1986) with relatively weak bonds among dispersed individuals (Di Fiore & Fleischer, 2005; Möller, 2012; Wikberg et al., 2012). The primates at Santa Rosa appear to fit this general pattern relatively well. In capuchins, females form stronger bonds than males as expected, showing a significant maternal kin bias in grooming during one study period (Bergstrom & Fedigan, 2013), and our long-term data show that mother–daughters and full-siblings form stronger relationships than other kin categories (Kalbitzer et al., 2017). Similar to previous findings from the Lomas Barbudal capuchins, females do not bias friendly behaviors to paternal siblings (Kalbitzer et al., 2017; Perry et al., 2008), and the more costly alloparenting behaviors, including nursing and carrying others' infants, were biased to maternal but not paternal kin (Sargeant et al., 2015, 2016). Female capuchins are categorized as displaying relaxed despotic dominance relationships with moderate kin bias (Bergstrom & Fedigan, 2013). Their dominance hierarchies are linear, with females entering the dominance hierarchy at approximately 6.5 years of age and assuming the rank immediately below their mother and, when applicable, their older sisters (Bergstrom & Fedigan, 2010). Female rank is relatively stable across an individual's lifetime, although rank reversals have been observed during our years of study following deaths or other disruptive events (Fedigan unpublished data, see also Manson et al., 1999).

Despite the frequency with which male capuchins change groups throughout their lifetimes (see above), they nonetheless form relatively tolerant and often affiliative relationships with one another (Jack, 2003b; Perry, 1998; Schoof & Jack, 2014). Such tolerant relationships, which are generally reserved for the philopatric sex (van Hooff & van Schaik, 1994; Patzelt et al., 2014), can partly be explained by the high rate of parallel dispersal discussed above (Wikberg et al., 2018). However, parallel dispersal is not necessarily sufficient to maintain tolerant relationships in other species (e.g., black-and-white colobus: Teichroeb et al., 2014; Wikberg et al., 2012, 2014), and these relationships likely evolved due to the costs and benefits associated with forming cooperative, neutral, or aggressive relationships that we discuss further in the section on reproductive success.

Spider monkeys at SSR also generally follow the expected pattern of strong male bonds and weak female bonds in species with female dispersal (Silk & Kappeler, 2017, but see Furuichi, Yamagiwa, & Aureli, 2015). Male philopatry leads to a high degree of familiarity among males from a young age facilitating the formation of strong relationships among them (Aureli & Schaffner, 2008). Indeed, proximity, grooming, and other friendly interactions are more common in male–male dyads than in female–female dyads (Fedigan & Baxter, 1984; Slater et al., 2009). Males also cooperate to defend the group territory, traveling more often than females at the territory boundaries (Chapman, 1990), possibly to patrol them (Di Fiore et al., 2010), and perform raids into neighboring territories (Aureli et al., 2006). Interestingly, and in stark contrast to male chimpanzees where dominance relationships are prominent with frequent aggressive interactions (e.g., Preis et al., 2019), male spider monkeys rarely exchange aggressive interactions with other males, a factor that, accompanied by the complete lack of submissive signals, makes it difficult to discern any dominance relationships among adult males (Aureli & Schaffner, 2008). Nonetheless, more subtle forms of male–male competition may exist in this species. In a principal component analysis using social interactions, embraces and aggression had a high load in the same component, which was categorized as "risk" (Rebecchini et al., 2011). Male–male dyads had higher scores than female–female dyads and female–male dyads not only in the component reflecting affiliation, as traditionally expected, but also in the risk component, contributing to the emerging view of a more ambiguous nature of male–male relationships in spider monkeys than previously thought (Rebecchini et al., 2011).

Despite the infrequent social interactions among female spider monkeys, our long-term research has uncovered many nuances about their relationships (Aureli & Schaffner, 2008). First, although females receive substantial aggression from other resident females during the first months after immigration (Asensio et al., 2008), especially from other recent immigrants (Riveros et al., 2017), there is little aggression among females with long tenure in the group (Riveros et al., 2017). Aggression by resident females against immigrating females is consistent with predictions that intra-group competition for food or other resources is costly to females (Schülke & Ostner, 2012; Snaith & Chapman, 2007; Sterck et al., 1997). While this pattern of aggression might suggest dominance effects, our long-term project has clearly shown this is driven by an initial, temporary hostile phase, and not due to wider dominance patterns (Asensio et al., 2008). The difference in group tenure appears to have another important consequence that is usually mediated by dominance in other species, access to high-quality food (Thompson et al., 2007). In SSR, the longer a female's tenure in her group, the better the quality of her core range in terms of food availability (Asensio et al., 2015). The second factor that modulates female–female relationships in spider monkeys is the presence of young infants. Several studies, including ours, have found an increase of embraces received by females with young infants (Eisenberg & Kuehn, 1966; Fedigan & Baxter, 1984; Schaffner & Aureli, 2005; Slater et al., 2007). We see similar effects in capuchin monkeys, where females with young infants receive a temporary spike in group centrality and tolerance from higher-ranking females (Kalbitzer et al., 2017).

5 | REPRODUCTIVE SUCCESS

Because of their relatively larger investment in offspring, female mammals are predicted to show little interindividual variance in lifetime reproductive success relative to males (Bateman, 1948; Clutton-Brock, 1988; Emlen & Oring, 1977; Trivers, 1972). Among long-lived animals, it takes decades of data collection to achieve the sample sizes needed to generate reliable estimates of lifetime reproductive success. Our capuchin data indicate that female reproductive success is impacted by a host of social, biological, and ecological factors including: age at death, the strength of her social relationships, the number of kin that reside in her group, the number/ratio of adult males that reside in the group, the frequency of alpha male replacements (and resultant infanticide events), and food resources available to her and her offspring over time (Campos et al., 2020; Fedigan et al., 2008; Fedigan & Jack, 2011; Kalbitzer et al., 2017). For example, the length of a female's interbirth interval decreases as the number of matrilineal kin present in the group increases (Fedigan et al., 2008). This may be due to the high rates of maternal infant handling and allonursing in this species, which are more common among maternally related kin (Sargeant et al., 2015, 2016).

In several species of primates, dominance rank (Majolo et al., 2012) and strength and/or number of social relationships (e.g., Ostner & Schülke, 2018) are positively related to offspring survival. In capuchins, however, this link is more complicated because of the frequent occurrence of infanticide committed by new alpha males (Brasington et al., 2017; Kalbitzer et al., 2017). Risk of infanticide by adult males varies extensively among primates, and numerous research efforts to understand the variation and evolution of this behavior have been undertaken (Henzi & Barrett, 2003; Lukas & Huchard, 2014; Palombit, 2012). Infanticide appears to be more common in species characterized by non-seasonal breeding, high reproductive skew and paternity certainty, and prolonged infant dependency, and numerous lines of evidence suggest that infanticide is an adaptive strategy for males (reviewed by Palombit, 2012). Female capuchins have an extensive range of strategies that are hypothesized to reduce infanticide, including unpredictable and concealed ovulation, situational receptivity, polyandrous and postconceptive mating, reproductive synchrony, mate choice, and alliances with resident males (Fedigan & Jack, 2013). Despite these strategies, infanticide is the leading source of infant mortality among capuchins in SSR and we have directly witnessed numerous cases (Brasington et al., 2017; Kalbitzer et al., 2017).

Our analyses of these events have found that offspring of higher-ranking and socially well-integrated females are more likely to survive during stable periods with no change in the alpha male (Kalbitzer et al., 2017), a finding that is similar to the relationship between rank/social integration and offspring survival generally observed in some other primate species (Majolo et al., 2012; Ostner & Schülke, 2018). However, during periods associated with changes in a group's alpha male, these more social and dominant females are at greater risk of having their infants killed by immigrant males (Kalbitzer et al., 2017). We attribute this to the increased proximity of high-ranking and highly social females to new males due to the central position in the group that these females maintain.

Infanticide by males has been reported for a number of spider monkey species, though it is still considered rare in the genus and has not been associated with changes in male dominance structure as is typical of other primates (Alvarez et al., 2015; Gibson et al., 2008; Teichroeb & Jack, 2017). Cases from outside of SSR described to date involved instances of males killing infants residing in neighboring groups (*N* = 2; Gibson et al., 2008) or adult males killing male infants residing in their own group (*N* = 8; Alvarez et al., 2015). While instances of infanticide have not been directly observed in the SSR spider monkey study group, preliminary analysis suggests that infant survivorship was negatively affected by the two cases of male immigration described above (Aureli, unpublished data). Collectively, these observations of infanticide and male dispersal between groups, accompanied by several reports of adult males killing subadult males residing in their own group (*N* = 3; Campbell, 2006a; Valero et al., 2006), indicate that male reproductive competition also negatively affects spider monkey female reproductive success, though the extent of this impact remains unknown.

Male reproductive success in mammals can vary widely and is dependent on multiple factors such as male condition (e.g., age, physiology, and health: Bercovitch et al., 2003), female strategies (Stumpf et al., 2011), a variety of social circumstances (e.g., maternal presence: Surbeck et al., 2019; social bonds and coalition partners: Schülke et al., 2010), and behavior and personality can play a role (e.g., Perry et al., 2017; Rosenbaum et al., 2018). Following capuchin males across their lives, we have been able to document extended periods of no reproductive output by males while they are subordinates interrupted by periods where these same males sire offspring during relatively short tenures in an alpha position. The reproductive success of males is largely dependent upon their ability to become an alpha male, and in our dataset consisting of 20 years of genetic and observational data, the most successful male sired over 24 infants (Fedigan & Jack, 2004; Wikberg et al., 2017, 2018). Because most alpha male capuchins monopolize reproduction, only about a third of the subordinate males sire any offspring (Wikberg et al., 2017, 2018). However, some subordinate males reside with, and provide coalitionary support to, their alpha male kin and thereby gain inclusive fitness benefits through the alpha male's reproductive success (Jack & Fedigan, 2004b; Wikberg et al., 2014, 2017).

When subordinate males do reproduce, it is often with the alpha male's adult daughters, which likely results from aversion to mating with close kin (Wikberg et al., 2017), similar to the pattern reported from the Lomas Barbudal capuchins (Godoy et al., 2016; Muniz et al., 2006). Cooperating with the alpha male, or at least forming a tolerant relationship with him, may allow these subordinate males to remain in the group and access these mating opportunities (Wikberg et al., 2017, 2018). A subordinate male that resides with a long-term alpha male and is able to produce offspring with the alpha male's mature daughters experiences reproductive success at levels similar to that of alpha males (Wikberg et al., 2018). This unexpected finding of high reproductive success for some subordinate males was revealed only after many years of study at our site and at Lomas Barbudal (Godoy et al., 2016; Muniz et al., 2006; Wikberg et al., 2017), a consideration for others when evaluating estimates of reproductive skew based on snapshots of short windows of time. Like other male-dispersed primate species (Silk et al., 2019), male capuchins likely switch among strategies, depending on age, group membership, and dominance rank. Being able to collect data from the same males as they age, disperse, and change dominance ranks is therefore necessary to assess their lifetime reproductive success. Long-term studies thus make an impactful contribution to our understanding of the nature of male reproductive strategies and lifetime reproductive success, and can also help us interpret patterns of genetic diversity in populations.

Reproductive skew among male spider monkeys is less steep than we observe in capuchins likely because reproduction is not mediated by dominance relationships and female choice plays a major role (Campbell, 2006b; Campbell & Gibson, 2008). The high degree of fission–fusion dynamics allows males to avoid overt competition for mating, as a single male and female can fission from the group to mate in secret (Campbell, 2006b; Gibson, 2010; Slater et al., 2008), possibly reducing the need to have well-established dominance relationships.

6 | LIVING AND REPRODUCING IN A SEASONAL ENVIRONMENT

The dry forests of ACG are among the most seasonal habitats in the tropics (Campos, 2018; Feng et al., 2013). Large oscillations in rainfall and temperature, concomitant with leaf shedding of trees and drying of water sources, lead to large shifts in the abundance of foods and the types of foods available, the availability of drinking water, and the thermoregulatory challenges facing the primates (Campos & Fedigan, 2009). We have been tracking the temperature and rainfall daily since the inception of our primate observations in the early 1980s. Additionally, since 2003, we have been monitoring the phenology of trees whose parts are consumed by the resident primates, and we have additionally conducted a transect study of old growth and regenerating forest around the administration area of SSR, recording 48,799 trees and saplings at least 1-m tall (Campos et al., 2014; Orkin, et al., 2019). By combining the phenology and transect data, we are able to estimate monthly fruit abundance in the home ranges of our study groups of capuchins and spider monkeys (Bergstrom et al., 2020). Taken together, this rich ecological dataset allows us to examine how intra- and inter-annual fluctuations in rainfall and linked productivity of the forest affect the resident primate populations.

Although inter-annual variation in overall fruit production can be large (Hogan & Melin, 2018), the mid-to-late dry season (March–April) is typically a period of high ripe fruit productivity, while the beginning of the dry season (November–December) and the early rainy season (June–July) are typically periods of low fruit productivity (Bergstrom et al., 2017). However, we join other researchers (e.g., Hanya & Aiba, 2010; Mitani et al., 2005) in cautioning against using rainfall as a proxy for fruit abundance, a practice that has been used in the past to model resource abundance in the SSR region before comprehensive data on food plant abundance and phenology were available (Chapman & Balcomb, 1998). Most tree species in SSR show marked seasonality in fruit production (Hogan & Melin, 2018) although *Ficus* trees are notable exceptions. Through their production of figs at irregular intervals, *Ficus* trees provide an important resource to primates and hundreds of other animal species, especially when other fruits are scarce (Hogan & Melin, 2018; Parr et al., 2011).

The primates inhabiting the dry forest of SSR show different responses to the seasonality of the forest. Spider monkeys, the most frugivorous of the three, exhibit fission–fusion dynamics (Aureli et al., 2008) in which they split into subgroups of variable size and composition for effective foraging (Aureli & Schaffner, 2008). In SSR, subgroup size is positively correlated with food availability (Asensio et al., 2009; Chapman et al., 1995). Spider monkeys also range in markedly different areas of the forest during different seasons (Asensio et al., 2012). Whereas there is high consistency in the location of the group's home range across years, core areas (i.e., areas of intense use) vary in size and location across seasons and years. This means that the yearly home range includes all the core areas from different seasons (Asensio et al., 2012). The pattern of variable core areas across time within a relatively stable home range could result from preferred usage of the areas currently most productive and at the same time the defense of future resources from other groups.

Capuchins in SSR remain in cohesive groups year-round and do not undergo fission during periods of low fruit abundance. Like spider monkeys, capuchins also shift their areas of use to track the availability of water and fruit patches (Campos et al., 2014), but switch their diet to rely more on insect and other invertebrate prey when fruit is less abundant (Melin et al., 2014; Mosdossy et al., 2015). In addition, capuchins also use floral resources seasonally, and for at least one common tree species, *Luehea speciosa*, their behavior (licking but not destroying flowers, presence of pollen on faces, moving from tree to tree in rapid succession, i.e., "traplining" behavior), together with morphology and nectar composition, suggests the capuchins may contribute to pollination of *L. speciosa* flowers (Hogan et al., 2016). Importantly, access to water is an important driver of home range use by capuchins (Campos et al., 2014; Campos & Fedigan, 2009), as they are the only primate in SSR that routinely drinks daily during the dry season rather than water from their foods (Chapman, 1988).

Despite these behavioral strategies, capuchin monkeys show evidence of energetic distress during periods of low fruit abundance. Research on female capuchins in SSR has demonstrated that periods of low fruit production correlate with indicators of metabolic stress, C-peptide, and urinary ketones, especially for pregnant and low-ranking females (Bergstrom et al., 2017, 2020). In addition, capuchins of both sexes exhibit elevated glucocorticoid secretion during periods of reduced access to food and water (Carnegie et al., 2011; Schoof et al., 2016). Our research on the gut microbiota of capuchins across seasons indicates that rainfall and diet have substantial effects on the diversity, composition, and function of the capuchin gut microbiome. The social group membership also impacts gut microbiome structure, although this effect may be weaker than seen among other wild primates (Orkin, et al., 2019; Orkin et al., 2019).

Given the seasonal fluctuations in food and water resources, it is perhaps unsurprising to see evidence of reproductive seasonality in the births of primates in the dry forest (Fedigan & Rose, 1995). Births peak at the beginning of the dry season (December–January) among spider monkeys (Aureli and Schaffner, unpublished data) and at the end of the dry season and early wet season (April–July) among capuchins (Campos et al., 2017; Carnegie et al., 2011). Unlike the extreme seasonality in births seen in ring-tailed lemurs and Verreaux's sifaka (Pereira, 1991; Richard et al., 2000), these peaks are not steep, indicating that births occur asynchronously and throughout the year in both capuchins and spider monkeys (Carnegie et al., 2011; Schaffner et al., 2012). Reasons for this might include high inter-annual variation in fruit production and rainfall (Hogan & Melin, 2018; Melin, et al., 2014) and, as discussed in detail above, the impact of infanticide by immigrating males.

By comparing data on fruit productivity to birth seasonality over many years, we observe that capuchin reproductive seasonality fits the predictions of the "maternal survival" model (Carnegie et al., 2011; Janson & Verdolin, 2005). According to this model, the mean peak in energy abundance will be aligned with the maximum energetic demands of lactation to increase maternal health and survival during this costly period. This strategy appears to be employed by some primate and other mammalian females. In other mammals, females appear to store nutrients during the months of high food abundance and then give birth after the mean peak in food abundance (Bronson, 2009). We have yet to examine whether spider monkey birth peaks coincide with periods of high fruit production but spider monkey mothers nurse their offspring well into the second year of the infant's life, and we have witnessed females nursing infants until their next offspring is born, spanning a three-year period (Schaffner, unpublished data). Whether spider monkeys show any reproductive seasonality or follow a more stable investment strategy over a long period of time, such as has been suggested for Bornean orangutans (van Noordwijk et al., 2013), will be an interesting question to examine in the future.

Over the past few decades, our data have spanned extreme climate events, such as drought, offering a rare opportunity to examine primate ecological, behavioral, and demographic responses. At SSR, as in many other tropical regions, inter-annual climate variability is strongly driven by the El Niño–Southern Oscillation (ENSO). By combining long-term life-history data with climate data, we have documented that ENSO-associated severe rainfall deficits are associated with declines in capuchin female fertility rates, high capuchin infant mortality, and disruptions in spider monkey female reproductive function (Campos et al., 2015, 2020). When considered in a comparative context with other primate species and populations around the world, such data provide invaluable information for modeling the impact of climate change and extreme weather events in tropical environments (Campos et al., 2017; Carvalho et al., 2019; Graham et al., 2016; Zhang et al., 2019).

7 | FORAGING ECOLOGY

Studies of dietary range and plasticity, food preferences, and feeding patterns strongly benefit from inter-annual research, as short-term studies under-represent dietary breadth (e.g., see Chapman et al., 2018), and indices of food selectivity are influenced by the availability of different foods, which varies within and across years. Our studies of the dietary ecology of sympatric primates in a well-characterized ecosystem have provided insights into how three sympatric primate species partition their dry forest habitats intra- and inter-specifically.

Howler, spider and capuchin monkeys occupy distinct but partially overlapping feeding niches. White-faced capuchins, the smallest of the three species, are highly omnivorous and have remarkable dietary breath (Bergstrom et al., 2018; Chapman & Fedigan, 1990; Fragaszy et al., 2004; Hogan & Melin, 2018). In SSR, we have observed them to eat primarily fruits (and some flowers and pith, but almost never leaves) from 144 species of plants and a wide range of invertebrates (Table 2; Melin et al., 2008). Searching for insects makes up about 70% of capuchin foraging time and 50% of ingestion events (Bergstrom et al., 2018; Melin et al., 2007). The spider monkey population at SSR has been observed to consume food items from 89 different plant species and is more frugivorous than capuchins, devoting approximately 71% of their feeding time to fruits, while supplementing their diet mostly with young leaves and flowers (Table 2). The only animals eaten regularly by spider monkeys are caterpillars (Chapman, 1988). The most folivorous of the three primates, the howler monkeys, have been observed to eat the leaves, fruits, and flowers of at least 71 plant species, which is almost certainly an underestimate, as it is based on by far the least amount of observational data (Table 2). A large component of our research program on primate feeding ecology involves asking how primates find and select their foods using their sensory systems.

8 | ADVANCES IN PRIMATE SENSORY ECOLOGY: COLOR VISION AS A CASE STUDY

Sensory ecology has long been involved in hypotheses of primate origins and adaptive radiation. Evolutionary anthropologists have used morphology of sensory structures to infer ancestral activity patterns and other aspects of behavior (Cartmill, 1992; Ross et al., 2007; Smith et al., 2007; Sussman, 1991). These hypotheses are strengthened by data on sensory behaviors, diets, and activity patterns of extant species. The important role that sensory systems play in the lives of wild primates is increasingly understood through studies uniting behavior, genetics, and models of sensory system function. Over the last 15 years, considerable advances have been made in understanding the surprising color vision variation among primates. Much of this progress has come from studying the capuchin, spider, and howler monkeys living in SSR (Kawamura, 2018). Unlike many other tropical forests, the observational conditions at SSR are remarkably good due to the relatively low, deciduous forest. Due to careful and complementary ecological studies, described in the previous section, we also have the necessary ability to control for food–tree phenology when comparing feeding rates among monkeys and to examine not only the impacts of receiver sensory variation on this short-term feeding, but also the effects on reproductive success. Through application and refinement of non-invasive methods for the isolation of primate DNA from feces, our research additionally unites examination of sensory gene sequences relative to other genomic areas to scan for evidence of natural selection (e.g., Hiwatashi et al., 2010; Orkin et al., 2020).

One of the derived characteristics of primates that has captivated biologists for decades is their trichromatic color vision—that is, a visual system based on three different cone types. With the emergence of a third cone type, primates have evolved a red-green color channel not present in other mammals (Jacobs, 2008; Lucas et al., 2003; Martin & Ross, 2005). Perhaps even more intriguingly, there is considerable variation within and among species in their capacity to distinguish different hues. With the exception of the completely colorblind owl monkeys (genus *Aotus*) and the routinely trichromatic howler monkeys (genus *Alouatta*), all primates living in Mexico, Central, and South America, have X-linked color vision variation (Dulai et al., 1999; Melin, et al., 2017). In this system, all males and typically a third to a half of females have dichromatic vision (red-green colorblindness). The link between opsin genotype and color vision phenotype is well established for primates, lending itself to natural experiments to test for impacts of color vision type on foraging, perception of social signals, or predator detection among individuals living in the same social groups (Changizi et al., 2006; Melin et al., 2012; Pessoa et al., 2014).

Like most monkeys in the Americas, capuchin and spider monkeys possess different alleles of the cone opsin gene (underlying primate color vision variation) and correspondingly different cone pigment tuning mechanisms resulting in different sensitivities to different wavelengths of light. In SSR, capuchins have 3 alleles, whereas two alleles are found among the spider monkeys (Hiramatsu et al., 2005). We have also discovered that spider monkeys at SSR differ from those in the Yucatan peninsula of Mexico in their opsin genes (Aureli & Matsushita, unpublished data). In howler monkeys, all males and females are trichromatic due to an opsin gene duplication; however, minor variations in the sensitivities of opsins are present among howler monkeys (Matsushita et al., 2014). Additionally, we found strong genetic evidence of balancing selection maintaining the opsin variation in capuchin monkeys and spider monkeys: the nucleotide sequences of the exons containing sites important for color vision tuning are more variable than the intron regions distantly located from theses exons and the "neutral reference" regions in the same genome in both species (Hiwatashi et al., 2010). This indicates that natural selection maintains the functional variation over the amount of opsin variation that would be present if the sites were evolving neutrally or under purifying selection (Hiwatashi et al., 2010).

Turning to behavior, there are noticeable effects of color vision type on foraging behavior. The strongest evidence for this is found among capuchin monkeys where multiple thousands of sequences of food investigation behaviors for a relatively large number of individuals (>80) across dozens of plant species have been examined. Trichromatic monkeys had higher feeding rates on reddish ripe fruits. Interestingly, the effect of trichromacy on feeding efficiency seems to be greatest among juvenile monkeys, whereas adults may learn to more efficiently use non-visual senses to forage; more research is needed in this area (Melin, et al., 2017; Melin et al., 2019). Color space models of food conspicuity using cone sensitivities for each species, and illumination profiles taken in SSR forest, suggest trichromacy should confer a detection advantage for important foods types including a majority of dietary fruits, flowers, and young leaves consumed by the three primates in SSR (Hiramatsu et al., 2008; Melin, et al., 2014; Melin, et al., 2017; Valenta & Melin, 2012). We also presented the first behavioral evidence that trichromats find small, ephemeral food patches, and likely experience a high finders' reward by depleting them before they are joined or displaced by conspecifics (Hogan et al., 2018; Melin, et al., 2017). Trichromacy may also be useful in narrowing down which fruits are ripe and desirable, although over short distances other sensory systems come into play (Hiramatsu et al., 2008, 2009; Melin et al., 2019).

Despite the predicted and demonstrated foraging advantages to monkeys with red-green color vision, analysis of fitness measures over the duration of the project for adult female capuchins indicates that trichromatic females do not have more offspring, more surviving offspring, or reproduce sooner than dichromatic females. This suggests that the color vision variation is not maintained in the population due to fitness advantages to trichromats (Fedigan et al., 2014). Importantly, this is *not* evidence that this variation is neutral. Rather, we have strong evidence from patterns of opsin gene diversity in SSR (Hiwatashi et al., 2010), not to mention the persistence of polymorphisms across millions of years in dozens of species, that color vision variation is maintained by balancing selection (Carvalho et al., 2017; Frentiu et al., 2007; Melin et al., 2012). Mechanisms of balancing selection, aside from heterozygous advantage, include niche divergence, frequency dependence, and mutual benefit of association. These hypotheses have not yet been extensively evaluated but seem promising, especially given that foraging benefits to trichromats are not ubiquitous (Caine et al., 2010; Melin et al., 2008; Melin, et al., 2014; Smith et al., 2012).

Dichromatic capuchin monkeys have an advantage in foraging for cryptic foods as evidenced by higher capture rates of surface-dwelling, camouflaged insects (Caine et al., 2010; Melin et al., 2010; Smith et al., 2012). Given that insects represent a considerable proportion of their diet, this advantage is non-negligible. Intriguingly, dichromats seem to rely more on non-visual senses during foraging, such as olfaction (Melin et al., 2009, 2019). This is a remarkable example of behavioral plasticity revealed through the "natural experiment" of having multiple sensory phenotypes living and feeding in cohesive groups of the same species. We are presently testing for niche divergence among monkeys in the same groups based on their color vision type to evaluate this possible mechanism of decreasing intra-group competition, which might favor the persistence of sensory variation over evolutionary timescales (Kawamura, 2018; Melin et al., 2008; Mollon et al., 1984).

The advantages (if any) of dichromacy to spider monkeys remain to be elucidated but may lie in search for cryptic fruits or predators among these specialized frugivores. As with capuchins and spider monkeys, studies of howler monkeys in SSR reveal that trichromats should have advantages for preferred foods types (ripe fruits). Unlike capuchins, however, howler monkeys eat leaves, not insects, to supplement their diets. Many key plant species have reddish young leaves, which are preferred by howler monkeys because they are softer, more proteinaceous, and easier to digest than mature leaves (Lucas et al., 2003; Melin, et al., 2017). It has been suggested that a ripe fruit diet, combined with fallback on reddish leaves, has favored the emergence of routine trichromacy in both howler monkeys and the ancestor of African and Asian primates. Field study of howler monkeys in SSR has provided independent support for this hypothesis. Importantly, given that the selective pressure(s) leading to polymorphic versus routine trichromacy likely vary, seeking a unifying explanation for the emergence of any form of primate trichromacy—a practice present in much of the historical literature—may be missing key distinctions between these systems. Study of sympatric primates with different color vision systems as found in SSR, together with comparative study of allopatric primates with the same color vision system (e.g., howler monkeys and catarrhines), may present a promising way forward (Melin, et al., 2017).

Promising areas of inquiry that remain to be addressed in primate sensory ecology include understanding plant–animal interactions more directly and their evolution. Opportunities offered by naturally occurring variation in sensory systems and behaviors of primate receivers, and signal variation via different food colors, odors, mechanical properties, tastes, and sounds are well-suited for examining how, when, and why different senses are used and the impacts of variation in signal structure. To date, we have shown differences in the taste receptors among our study species in SSR and elsewhere (Tsutsui et al., 2016), and among the behaviors, genes, and morphology associated with the olfactory sense (Veilleux et al., 2019). Our work examining the interplay among sensory systems is also in its infancy (Melin et al., 2019), and future work will explore these topics within and between species.

9 | CONSERVATION AND EDUCATION INITIATIVES

Around the world, primate populations are increasingly at risk: 75% of primate populations are declining, and over 60% of species are considered to be threatened with extinction (Estrada et al., 2017). While the specific threats differ by region, they are all anthropogenic in origin: habitat loss and degradation, climate change, hunting, and capture for the pet trade are chief among them (Almeida-Rocha et al., 2017; Estrada et al., 2017; Kalbitzer & Chapman, 2018). Yet, hope remains, and researcher presence can deter active threats (e.g., poaching, habitat loss) and serve as "umbrella" protection to the ecosystem at large (see Wrangham & Ross, 2008 for detailed analysis of the conservation benefits of long-term research). Perhaps most importantly, it is near-impossible to successfully run a long-term research program without establishing strong and meaningful relationships with local stakeholders. These relationships can benefit the local communities (e.g., employment and education opportunities, the prestige of local projects and protected areas) as well as the researchers (e.g., access to traditional knowledge and improved logistic outlooks; Durant et al., 2007; Kasenene & Ross, 2008; Pusey et al., 2007). Friendly relationships with government officials can also result in the establishment of protected areas and legislation (Wrangham, 2008), and evidence suggests that long-term research contributes disproportionately to environmental policy (Hughes et al., 2017).

In this regard, ACG is a success story (Janzen, 2000) and one that is at least partly due to the myriad of long-term research projects ongoing within its boundaries (data from many of which are summarized in this issue). Ecological research in the remnant fragments of tropical dry forest surrounding the historic "Casona" in Santa Rosa National Park led to advocacy for improved conservation measures, political action, and ultimately the protection of large swaths of cultivated land, which were allowed to regenerate. The effect of forest protection and regeneration on the local primate populations in SSR has been unmistakably positive: Capuchin and howler populations grew quickly, eventually stabilizing at approximately twice their original numbers (Fedigan & Jack, 2001, 2012). Since primates provide critical seed dispersal and pollination services in the dry forest and other tropical ecosystems (Chapman, 1995; Hogan et al., 2016; Valenta & Fedigan, 2008), the growing populations of these species may, in turn, contribute to the regeneration of the forest in ACG (Chapman et al., 2020). We do not have similar data for spider monkeys, as their high degree of fission–fusion dynamics makes it more difficult to assess population size with traditional techniques, but we continue to test different methods for collecting and analyzing spider monkey survey data, including drones with thermal cameras (Spaan et al., 2017; Spaan, Burke, et al. 2019; Spaan, Ramos-Fernández, et al. 2019).

The conservation benefits of our research extend beyond direct protection of the primates and their habitat living in SSR. Our study groups range in the tourist areas, providing us opportunities to engage with numerous local and foreign tourists and student groups. In recent years, increasing tourism in ACG has seen a rise in capuchins accessing human-sourced foods from garbage cans (https://www.acguanacaste.ac.cr/biodesarrollo/huella-verde). High tourism in other regions of Costa Rica has led to high rates of primate-sourced food theft and direct contact, increasing the health risk to humans and monkeys alike (McKinney, 2014; Russon et al., 2014). Primatologists are working with ACG administration and SSR ecotourism experts to contribute recommendations about "best practices" that are passed on to visitors, such as the development of the "Quiero Dejar Una Huella Verde" ("I Want to Leave a Green Footprint") project in 2016 by SSR staff and primatologists. This project's goal was to more effectively manage the garbage and recycling accumulating in SSR and other ACG sectors, which was quickly leading to problematic foraging behaviors by capuchins and other wildlife. In addition to a successful public outreach campaign designed to raise awareness of proper waste disposal, this project led to the installation of new waste receptacles throughout ACG, preventing animal access to food scraps and diverting recyclable materials out of the landfill.

Yet, there is still much more to do, and many areas to improve in the realms of training programs, education, and collaboration. Given the importance of this site on many levels—its role in knowledge generation, the intrinsic value of the forest and animals, its status as a World Heritage Site, and the rare and critically endangered forest biome—it is imperative that we continuously build upon past and current efforts to protect this irreplaceable forest and its inhabitants.

10 | CONCLUSIONS

In today's age of widespread deforestation and anthropogenic disturbance globally, ACG has been an outlier and a positive, forceful example of ways that reforestation and conservation can succeed through collaboration via local, regional, national, and international communities spanning academia, government, and paraprofessional resident Costa Ricans (Janzen and Hallwachs, this issue). Over the past 37 years, primatologists in ACG have integrated study of plant community ecology, drought, population biology, and genetics, with fine-grained behavioral observations to ask and answer questions about the demography, social relationships, foraging ecology, conservation, community ecology, and more. This integrative approach has improved our ability to understand the adaptation and evolution of our study species specifically as well as primates and their habitat more generally. The progress we have made in studying the life history, social dynamics, foraging ecology, and impacts of climate on primate health, behavior, and population trends would not have been possible without detailed, continuous study of these long-lived species. Through comprehensive and multifaceted study at a single location, we can integrate vastly different kinds of data touching on multiple levels of biological organization within a species, interactions among species, and interactions between the community and ecosystem, into a more comprehensive whole. Importantly, this work has practical and primate conservation contributions as well. For example, information on diet and food preferences will inform potential reforestation initiatives to emphasize species important for feeding. Finally, by our membership in the broader ACG community, other researchers can benefit from data originally collected to study primates. For example, our historical data on tree abundance in monkey home ranges enabled a study on bird community recovery with forest succession (Owen et al., 2020). Likewise, primatologists have strongly benefited from data collected by others, such as comprehensive climate data. Moving forward, we strive to expand and integrate data sharing across projects and to increase direct collaborations among the researchers studying vertebrate and invertebrate communities, vegetative ecosystems, and community ecology to fuel new discoveries and to optimize and reinforce conservation and education initiatives.

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DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no data were created or analyzed in this study.

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