19   Colobine Population Ecology

What Limits Population Size

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Introduction

A fundamental issue in ecology is determining factors that influence animal abundance. The importance of this theoretical issue has taken on new significance with the need to develop informed management plans for endangered and threatened species. This need is driven by the rapidly rising rate of biodiversity loss; the current extinction rate is approximately 1000 times higher than background rates (Pimm et al. 2014) and estimates suggest that at least 322 vertebrate species have gone extinct since 1500 and that surviving vertebrate species have declined in abundance by 25% since 1970 (Dirzo et al. 2014). Overall, 60% of all primate species are currently threatened with extinction (Estrada et al. 2017) and while it remains to be confirmed, it seems almost a certainty that with the disappearance of Miss Waldron's red colobus (*Procolobus waldronae*) in West Africa (Oates et al. 2016), we have lost the first primate in the last century.

Although the threats to primates are numerous, habitat loss is thought to be the most significant. Global forest loss between 2000 and 2012 was estimated at 2.3 million km^2, with an increase of 2101 km^2 every year in the tropics (Hansen et al. 2013). To put this in perspective, an area approximately the size of the Democratic Republic of Congo was lost in 12 years. This forest loss is primarily driven by increasing human populations and high consumption rates (Crist et al. 2017; Kalbitzer and Chapman 2018). The world's population is expected to rise from 7 billion in 2011 to almost 10 billion in 2050 (United Nations 2009). Globally, agricultural lands expanded by 48,000 km^2 between 1999 and 2008 (Phalan et al. 2013) – an area slightly less than the size of Costa Rica.

If this was not enough, many primate populations, if not the majority, are severely reduced by hunting. Global evaluations of wildlife exploitation are extremely poor; however, in the Congo Basin alone, four million tons of bushmeat are estimated to be harvested each year (equivalent to approximately 4,500,000 cows, or 80 million small (5 kg) monkeys, of course not all bushmeat is primate, Fa and Brown 2009). Primates are also threatened by the changing climate that human actions have caused (Chapman et al. 2020). Temperatures are predicted to increase by $1.5°C$ by the end of the twenty-first century (IPCC 2014) and researchers have projected that by 2100 75% of all tropical forests present in 2000 will experience temperatures that are higher than

This chapter includes Electronic Supplementary Material (ESM) at: www.cambridge.org/colobines

the temperatures presently supporting closed canopy forests (Wright et al. 2009; Peres et al. 2016). Addressing how to respond to these risks is one of the fundamental questions of both applied conservation and primate population ecology.

Population ecology is the study of the factors affecting population size and structure, and how and why a population changes over time. The theoretical framework of the field is grounded in questions dealing with population growth, regulation, dynamics and demography. The theory has been developed with studies of a variety of organisms including humans, mammals, birds, disease organisms, and micro-organisms and it has been applied to issues such as wild-harvested fish stocks and dynamics of logged forest stands (Holmes 1995; Sinclair 2003). Ideally, studies quantify change in populations over time and identify the drivers of that change either through experimentation or by identifying factors that change in unison with the population change (Krebs et al. 1995). Because of the slow life histories of primates (Van Allen et al. 2012) quantifying their population changes through long-term studies can rarely be achieved (Chapman et al. 2017). Thus, static approaches are more common, such as comparisons across populations experiencing different ecological conditions, not the fluctuations in population size or composition over time.

The overall goal of our work it to explore the relative importance of potential drivers of colobine population change with the aim of providing information for future conservation efforts. To meet this goal, our first objective is to describe variables influencing colobine population ecology in both Asian and African colobines. Our second objective is to describe small-scale temporal and spatial variation in colobine populations and ecology in Kibale National Park, Uganda (hereafter Kibale), where CAC has conduct long-term research. We summarize our Kibale findings to understand the magnitude of the variation that can occur on small spatial and temporal scales where ecological variables (e.g. forest composition, predator populations) remain more similar than on larger scales (e.g. comparisons among regions). Our final objective is to use this information to ask the fundamental question: What limits colobine population size? Here, we place an emphasis on illustrating where high-quality data are available and where knowledge gaps exist. We emphasize these gaps in the hope of motivating researchers to gather new data aimed at answering these fundamental questions more accurately and providing better information to conservationists trying to apply this knowledge.

Colobine Diet and Population Characteristics

Over 40 African and Asian colobine species have been studied at more than 75 sites, with some sites being studied across multiple years (ESM Table 19.1). As a whole, these data highlight the tremendous diversity of colobine social organization, ranging behaviour and diet. Population density and mean group size are variable in both African colobines and Asian ones (Figure 19.1). Population density ranges from 3 ind/km² (*Colobus angolensis*; Ituri, DRC) to 784 ind/km² (*Procolobus kirkii;* Jozani – cultivated land, regenerating forest) in African colobines and from ~ 2 ind/km² (*Semnopithecus schistaceus*; Junbesi, Nepal) to 220 ind/km² in an
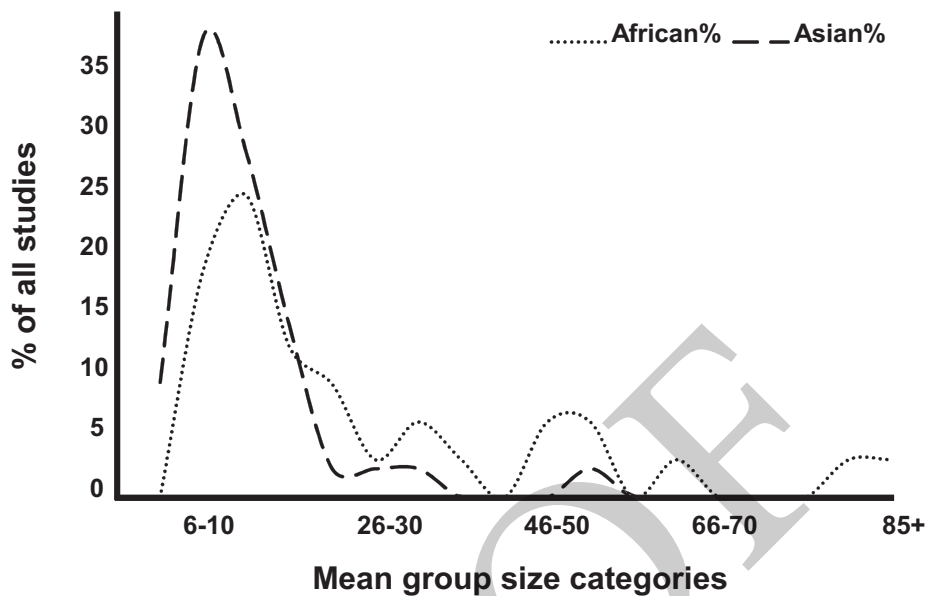
Figure 19.1 Mean group size of African and Asian colobines. Data from ESM Table 19.1 and for presentation groups were placed into bins of five, and a smoothing curve was applied to visualize intermediate group sizes.

Asian colobine, *Simas concolor*. The majority of Asian colobines studied (25/33) had a density of 50 or fewer ind/km². while a little more than half (13/25) of African colobine groups had between 50 and 300 ind/km². Similarly, while most groups studied had a mean group size of 25 or fewer individuals (22/35 African; 38/41 Asian), group size ranged from 6 individuals in *Colobus guereza* in a fragment at Kibale, Uganda to more than 300 individuals in *Colobus angolensis* at Nyungwe, Rwanda (Figure 19.1). In comparison, Asian colobines mean group size ranged from 3 individuals in *Presbytis potenziani* and *Semnopithecus concolor* (both at Sarabua, Indonesia) to 54 individuals in *Semnopithecus dussumieri* at Kaukori, India. Although the range in mean group size is smaller for Asian than African colobines, some Asian species do associate in large bands ranging from 175 to 450 individuals (e.g. *Rhinopithecus* spp.).

While more than half of the species studied have home ranges of 100 ha or smaller (25/30 of African colobines; 23/35 of Asian colobines), African colobine home range size varies from 0.5–1.2 ha in *Procolobus kirkii* in the mature and regenerating forest of Kiwengwa, Zanzibar, to 2440 ha in *Colobus angolensis* in Nyungwe, Rwanda. In Asian colobines, home range variation is even greater, ranging from 2 ha in *Semnopithecus vetulus* at Polonnaruwa, Sri Lanka, to 3500 ha in *Rhinopithecus brelichi* at Fanjingshan, China. Variation in day range is also extensive, varying from 310 m in *P. kirkii* at Jozani, Zanzibar (cultivated land, regenerating forest) to 1212 m in *Procolobus verus* at Taï National, Ivory Coast.

In addition to interspecific variation, there is also a high degree of intraspecific variation in colobine home range use and population density. For instance, the African *Colobus guereza* has a home range of 100 ha and a density of 17 ind/km² in Ituri, DRC, but a home range of 28 ha and a density of 100 ind/km² in Kibale (Kanyawara; 1971–72), Uganda. Similarly, *Procolobus kirkii* has a home range of 13 ha, a density of 784 ind/km² and a day range of 310 m at one site of cultivated land and regenerating forest in Jozani (1999), and a home range of 60 ha, density of 100 ind/km² and day range of 1044 m at another forested site in Jozani (1980–81). Similarly, in India, the *Semnopithecus dussumieri* home range is 20 ha and density 121 ind/km² in Gir, but home range is ~775 ha and density 3 ind/km² in Kaukori.

Just as colobine group sizes and ranging are highly variable, colobine diets are also variable. More than 50% of the diet of most African colobines (38/53) and half of the Asian colobines is composed of leaves, highlighting the highly folivorous nature of the colobine clade. Overall, most colobine diets were composed of less than 20% of mature leaves (African 43/51; Asian 18/27) and between 26% and 75% of young leaves (African 37/51; Asian 18/29). Seeds and fruits accounted for less than half (<50%) of the diet of both African (50/53) and Asian (30/37) colobine species. In most cases (African 42/53; Asian 27/34), flowers accounted for less than 10% of the diet. Despite a generalized dietary reliance on leaves, some colobine species rely heavily on entirely different food sources. For *Rhinopithecus bieti* at three study sites (Wuyapiya, Samage-Baimaxueshan, Tacheng-Yunnan; China), between 60 and 94% of the diet was composed of 'other', a food category principally represented by lichens.

There can also be extensive variation in these parameters at the same location among groups or within the same population over time (ESM Table 19.2). For example, within Kibale there is extensive variation in population characters in red colobus (*Piliocolobus tephrosceles*) and black-and-white colobus (*Colobus guereza*), with red colobus exhibiting more variation than black-and-white colobus. Group size in black-and-white colobus has been reported to range from 4 to 11 individuals, while the group size of red colobus ranges from 14 to 152 individuals (Chapman et al. 2002a; higher value CAC, pers. obs.). Similarly, diet was highly variable. Young leaf consumption in red colobus in Kibale ranged among groups from 14.8% to 84.9% of time spent feeding, while young leaf consumption only ranged from 45.1% to 89.7% among black-and-white colobus groups. The cause of the greater variation in the diets of red colobus is not known, but it may relate to larger group sizes in red colobus resulting in greater variation in the range of individual feeding decisions.

Food Resources

Protein-to-Fibre Model

By far the most commonly tested and best supported model for predicting colobine biomass is the 'protein-to-fibre model'. Based on observations of Central American howler monkeys (*Alouatta palliata*), Milton (1979) proposed that an important

criteria in leaf selection was the protein-to-fibre ratio, with leaves with higher protein-to-fibre ratios being selected over those with lower ratios (see Matsuda et al. 2013 for data on selection by two Bornean colobines). Because the digestion of fibre requires fermentation by symbiotic microbes, fibre is often considered an antifeedant as this process is slow, with insoluble fibre (cellulose, hemicellulose, and lignin) being only partially digestible (McNab 2002; Cancelliere et al. 2018; Rothman et al. 2015; Rothman et al. 2012). Furthermore, nitrogen is a limiting nutrient in many environmental systems. Since nitrogen is predominantly found in protein, herbivores should compensate for this limitation by choosing foods high in protein (White 1993). Waterman et al. (1988) suggested that the biomass of folivorous colobines could be predicted by the weighted contributions of the protein-to-fibre ratio of mature leaves of the most abundant trees in a particular habitat. Subsequently, this index of dietary quality has been successfully applied to predict the biomass of small-bodied folivorous monkeys at local (Chapman et al. 2002b; Ganzhorn 2002) and regional scales (Oates et al. 1990; Waterman et al. 1988; Davies 1994; Chapman et al. 2004; Fashing et al. 2007a) (Figure 19.2).

The mechanism by which this index operates to determine folivore biomass is not clearly understood. Davies (1994) suggested that colobines fed on mature leaves with high protein levels and little fibre when other preferred foods were unavailable, and thus reliance on mature leaves could support high population densities that would otherwise be limited by periods of food scarcity. However, some colobines (e.g. *Piliocolobus tephrosceles*) rarely consume mature leaves because young leaves are always available, yet this index is still a good predictor of their biomass (Chapman et al. 2004). One potential explanation is that the protein-to-fibre ratio of mature leaves in an area is correlated with the protein-to-fibre ratio of foods in general. This idea is supported by data from Kibale, where the protein-to-fibre ratios of mature and young leaves are strongly correlated ($r = 0.837$, $P < 0.001$) (Chapman et al. 2004).

While these studies suggest that the protein-to-fibre ratio of leaves is a critical factor limiting folivorous primate population sizes, there are reasons to be cautious and to avoid premature implementation of this idea into management plans. This scepticism is based on four main factors. First, studies attempting to empirically verify the protein-to-fibre model are correlative, and it is quite possible that this ratio is related to another, as of yet undetermined factor (Chapman et al. 2010a; Chapman et al. 2010b; Wallis et al. 2012). Second, protein concentrations of ingested leaves are higher than species' estimated requirements (Rothman et al. 2011; Oftedal 1991). Third, we should use available nitrogen to evaluate this nutritional model. However, studies typically measure total nitrogen, which may be problematic since tannins and fibre-bound nitrogen likely reduce the availability of nitrogen in most folivore foods in unpredictable ways (Wallis et al. 2012; Rothman et al. 2008a; Rothman et al. 2012). Finally, new empirical data call into question the generality of this model. For example, in spite of changes in the protein-to-fibre ratio of mature leaves resulting from changes in forest composition (i.e. changes in density of specific species), there were no detectable changes in the
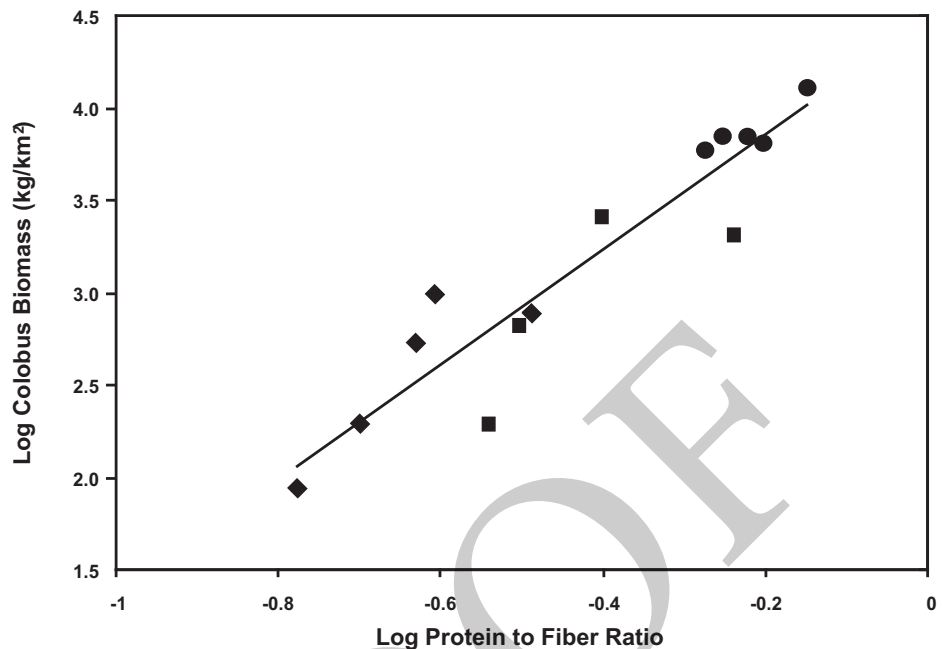
Figure 19.2 The relationship between mature leaf chemistry and colobine biomass at rainforest sites in Africa and Asia. Chemical values are weighted mean percentages of dry mass, standardized to the species basal area to account for different proportions of the flora being sampled at each site. The weighted values were calculated from $\Sigma\ (P_i + X_i)/\Sigma\ P_i$, where P_i is the proportion of the basal area contributed by species i and X_i is the chemical measure for species i. This figure is standardized to 100%. Diamonds are sites from around the world (Oates et al. 1990); squares are forest sites within Kibale National Park, Uganda (Chapman et al. 2002b); and open circles are the forest fragments studied from Kibale National Park, Uganda.

population size of red colobus in Kibale (Chapman et al. 2010a; Chapman et al. 2010b). Another example that is inconsistent with model predictions focuses on populations living in regenerating habitats, where leaves have higher protein-to-fibre ratios and lower levels of secondary compounds than old-growth forest trees (Coley 1983). The model predicts that regenerating forests should support increased female fecundity, as evidenced by populations with a greater number of infants per female than populations in old-growth forest. A study in Kibale reports that leaves have higher protein-to-fibre ratios in regenerating habitat, but there was no corresponding difference in the demographic structure of red colobus groups in regenerating versus old-growth forest (Gogarten et al. 2012).

These methodological issues, combined with limited empirical support in the recent studies discussed above, raise doubt as to the general applicability of this model. Further studies are needed to examine under what conditions the model applies and when it does not.

Composition of the Forest

Leguminous trees are an important food source for Southeast Asian colobines. A comparison across nine sites throughout much of Southeast Asia revealed a correlation between the abundance of leguminous trees and colobine biomass in the region (Davies 1994), which could be because of the high protein content typically associated with this type of tree. Alternatively, since there is a negative relationship between the abundance of leguminous versus Dipterocarp trees, it may be that without Dipterocarps the forests are richer and this is what drives the increase in colobine abundance (Davis 1994). However, an analysis of the relationship between African colobine abundance and leguminous trees is not significant (Davies 1994), despite a demonstrated preference for seeds and young leaves of species in this taxonomic group (McKey 1978c; Maisels et al. 1994).

The relationship between leguminous trees and Asian colobine biomass is similar to that found for some frugivores with respect to figs. For example, fig density correlates with the density of orangutans (*Pongo abilii*) and gibbons (*Hylobates* spp.) (Wich et al. 2004; Marshall and Leighton 2006). This positive relationship might be expected because figs contain many essential nutrients and minerals (O'Brien et al. 1998), thereby providing a nutritionally balanced staple food in some areas (Felton et al. 2009; Felton et al. 2013). But as with leguminous trees, the relationship between figs and frugivorous primate density is mired in controversy. Stevenson (2001) assembled data on fruit production and primate abundance from 30 neotropical sites and found no relationship between fig abundance and primate biomass.

Environmental Disaster Causing Food Shortages

Colobine populations could be limited by environmental disasters or unusual environmental events causing dramatic reductions in the food supply. Dittus (1985a) described the effect of a cyclone that cut across the island of Sri Lanka on 23 November 1978. Overall, 46% of all of emergent and upper canopy trees were killed, as were 29% of understory trees. The two colobines found in the area (*Semnopithecus entellus* and *Trachypithecus vetulus*) subsequently over-browsed a number of the remaining trees, resulting in additional tree mortality (Dittus 1985b). The short-term impact of the resulting decrease in food supply was smaller than one might expect, with population declines of only 5% for *S. entellus* and 5%–10% for *T. vetulus* within one month after the cyclone.

Some of the best long-term data on folivore populations are those on the howler monkeys (*Alouatta palliata*) on Barro Colorado Island (BCI), Panama. It should be noted that while howlers have anatomical adaptations for eating leaves, they are heavily reliant on, and appear to prefer, fruit (Pavelka and Knopff 2004). On BCI, fruiting, flowering and leaf set can be disrupted if the rains deviate from their typical seasonal pattern, which has happened five times between 1929 and 1979 (Foster 1982). Following an unusual rainfall event that caused severe fruit crop failures in

1970, howler monkey mortality increased. Despite this there is no evidence that this led to any long-term population crash (Milton 1982; Milton et al. 2005). Another long-term dataset on the population dynamics exists for red colobus and black-and-white colobus in the old-growth forest of Kibale. Over 45 years, during which no ecological disasters occurred, the populations of both species appear stable or gradually increasing (Struhsaker 1997; Chapman et al. 2010b; Chapman et al. 2015; Chapman et al. 2018a; Chapman et al. 2018b).

For natural disasters to limit populations, they would have to occur at a frequency greater than the population's ability to recover. Possibly the most frequent type of natural disaster affecting many forests are hurricanes or cyclones. Hurricane activity varies geographically. For example, between 1920 and 1972, Madagascar was hit by 362 hurricanes (7.0/year) (Ganzhorn 1995). Between 1871 and 1964, an average of 4.6 hurricanes affected the Caribbean each year (Walker et al. 1991). In contrast, mainland Africa is infrequently affected by hurricanes (Chapman et al. 1999). When Hurricane Joan touched land in Nicaragua, 80% of the trees were felled (see also Boucher 1990; Pavelka and Behie 2005), thus the effect of hurricanes on forest systems can be dramatic. However, the probability of a hurricane or cyclone influencing the same population on a frequent basis is unlikely. For example, for the whole island of Puerto Rico, which is in an area of high hurricane activity, the return time is 21 years, thus the chances of a single population being affected twice in a short period of time is low (Dittus 1985a). Given that, where data are available, colobine diets seem quite flexible – possibly mitigating their ability to survive brief ecological crunch periods – and that the probability of a natural disaster hitting the same population multiple times at relatively short intervals is quite small, it seems unlikely that these events limit colobine population size.

Intraspecific Competition

Research on primates have made significant advances with respect to understanding how competition with and between groups of the same species shape a population's behavioural patterns and social organization (Wrangham 1980; Sterck et al. 1997) and recent research on colobines have led to new insights (Snaith and Chapman 2007; Koenig and Borries 2006). This research has taken on a very behavioural flavour examining variables like within-group aggression and day length as a function of group size or food availability (Snaith and Chapman 2008; Teichroeb and Sicotte 2018). As such this body of research has typically supported the importance of food availability as a determinant of population size, which we have previously discussed. For example, folivores have been demonstrated to deplete the resources within a single tree (patch) through their feeding and the speed of patch depletion is a function of patch size and the number of feeding individuals (Tombak et al. 2012; Chapman 1988). Similarly, colobus monkeys have been shown to compete more over food (within-group scramble and between-group competition) when food is scarce (Teichroeb and Sicotte 2018).

Interspecific Competition

Two or more colobine species are found at a number of field sites and at some sites there is considerable dietary overlap between the species (e.g. Kibale – *Colobus guereza* and *Piliocolobus tephrosceles*; Chapman et al. 2002a), while sympatric species at other sites have markedly different diets (e.g. Kuala Lompat – *Presbytis melalophus* and *Trachypithecus obscurus*; Davies 1994). In most situations, it is unlikely that colobines will overlap significantly in diet with cercopithecine monkeys or apes, although at some Asian sites they share some fruit resources (Davies 1991). In Africa, overlap is typically much less. For example, the diet of redtail monkeys and red colobus of Kibale overlapped by only 19.2% of their foraging time despite spending a great deal of time in mixed-species groups (Chapman and Chapman 2000b, 1996). These results suggest that interspecific food competition is low among African colobine and cercopithecine primates.

However, there are a number of reasons to be sceptical about drawing interpretations about competition from these data. First, it could be that competition is only significant during periods of food shortages, such that the available data may be inadequate for detecting competition. Since periods of food scarcity can be decades apart, interspecific competition can be an important, undetected, selective pressure on population dynamics, foraging strategies, digestive physiology and anatomy. Second, there can be a large amount of spatial and temporal variation in diet and this can greatly influence measures of dietary overlap used to evaluate the potential for competition. For example, Struhsaker and Oates (1975) studied red colobus and a black-and-white colobus groups with adjacent home ranges and found dietary overlap to be 7.1%. A similar study by Chapman et al. (2002a) calculated dietary overlap for the two neighbouring groups of red colobus to be 37.3%, while that between red and a black-and-white colobus group was 43.2%, when the black-and-white colobus group's home range fell entirely within the home range of the red colobus group – the scale at which competition actually occurs. These values suggest that we should re-evaluate interpretations from studies of dietary overlap that involve interspecific contrasts of groups that occupy different areas or groups of different species studied at different times. Third, competition can only occur if the resource is limiting. While there are studies showing patch depletion in colobines (Snaith and Chapman 2005; Tombak et al. 2012), there is no study to our knowledge that clearly demonstrates that a population is limited by the availability of a particular resource. Given the scientific evidence needed to demonstrate competition (Connell 1980), it is the authors opinion that the scientific community has not obtained conclusive evidence for the role of competition in limiting colobine populations. However, there is one study in cercopithecines that is suggestive of competition (Houle et al. 2006). Houle et al. (2006) demonstrated that socially dominant primate species could exclude subordinate species from resources, such that the subordinate species tended to feed in the tree after the dominant one had left resulting in lower feeding returns for the subordinate species (higher give-up-times). However, the smaller subordinate species often found fruiting trees before the

dominant species did, a mechanism that may enable coexistence. But the potential for competition for fruit might be very different from that for leaves.

Predation

While there are a number of anecdotal descriptions of predation on colobines in both Africa and Asia (reviewed by Davies 1994), only a handful of studies report long-term data on colobine predation rates. In Africa and Asia there are large eagles that are known to prey on primates. In Kibale, three studies have examined the impact of crown-hawk eagles on colobine predation (*Stephanoaetus coronatus*; see also anecdotal reports in (Cordeiro 1992; Maisels et al. 1993; Gautier-Hion and Tutin 1988; Shultz et al. 2004; Shultz 2002) in areas where the colobine density was known. In an 11-month study, Skorupa (1989) found the bones of five black-and-white colobus and three red colobus below the nest of a pair of eagles. In a 39-month study of a single nesting pair, Struhsaker and Leakey (1990) estimated that the minimum percentage killed per year for red colobus males was 0 and 0.047 for females, and <1.08 for male and 0.047 for female black-and-white colobus. Finally, in a 37-month study of the remains under two nests, Mitani et al. (2001) found evidence of four black-and-white colobus and nine red colobus. It is difficult to know the impact of crown-hawk eagles in general since the territories of the birds are not known [estimates range from 3.8 km^2 (Mitani et al. 2001) to 10 km^2 (Struhsaker and Leakey 1990)]; however, given the density of the colobines, their potential reproductive rates, and the pressure exerted by other predators in Kibale (e.g. chimpanzees), it seems unlikely that crown-hawk eagle predation is a limiting factor for these colobine populations. A study of 16 nests in Taï Forest, Ivory Coast, monitored over different periods of time found the remains of 31 *Piliocolobus badius*, nine *Procolobus verus*, and nine *Colobus polykomos* (McGraw et al. 2006), but the time frame over which these animal's remains were deposited was unknown.

In many locations where primates are studied, large felid predators have been hunted to local extinction or their numbers are dramatically reduced; however, there is some interesting data on felid predation from Taï National Park, Ivory Coast. Two studies have conducted faecal analyses and have found colobine remains in leopard (*Panthera pardus*) dung (ESM Table 19.3) (Zuberbuhler and Jenny 2002; Hoppe-Dominik 1984). Interpreting these data is not straightforward and determining actual rates of predation is not possible. Nonetheless, these data suggest that colobines may be frequently preyed upon, indicating that more information is needed on predation by felids at natural densities to understand their impact on colobine populations.

Despite the lack of conclusive evidence that avian or felid predators limit colobine populations, there is clear evidence for the importance of predation by chimpanzees (*Pan troglodytes*) at some, but not all, locations. Davies (1994) presents an excellent review of the early studies of chimpanzee predation of red colobus (Boesch 1994a; Uehara 1977; Takahata et al. 1984), showing that chimpanzees kill a large proportion of the population at some sites, but not at other sites. A 40 month study from Gombe

reported that chimpanzees killed between 20% and 40% of the population (Wrangham and Bergmann-Riss 1990). One would imagine that such high predation rates would drive the red colobus to extinction, but it has not.

More recent studies indicate that chimpanzee predation on red colobus correlates with changing red colobus population density at Ngogo field site in Kibale. The very large chimpanzee community there preys heavily on red colobus (Mitani and Watts 1999; Mitani et al. 2002). The high level of predation corresponded with a steep decline in red colobus numbers as indicated by census data (Lwanga et al. 2011; Teelen 2007b). Fortunately for the endangered red colobus population of Kibale, large new areas have become available through forest restoration that are suitable for red colobus (Omeja et al. 2012). Thus, the red colobus population throughout the park is increasing (Adamescu et al. 2018; Chapman et al. 2018a; Chapman et al. 2018b)

Disease

Disease can clearly cause short-term reductions in primate population size (Milton 1996; Collias and Southwick 1952; Work et al. 1957). For example, a 50% decline in the howler monkey (*Alouatta palliata*) population on BCI occurred between 1933 and 1951 and was attributed to yellow fever (Collias and Southwick 1952). Over 5000 gorillas are thought to have died from Ebola during a single outbreak (Bermejo et al. 2006). In the Namib desert, heavy tick infestations (*Rhipicephalus* spp.) were speculated as the cause of infant mortality for more than half (*n* = 18) of recorded chacma baboon deaths (*Papio ursinus*) (Brian and Bohrman 1992). Rudran and Fernandez-Duque (2003) quantified demographic changes in a population of red howler monkeys (*Alouatta seniculus*) over 30 years and reported a 74% population decline that they attributed to disease.

Given the high number of studies on colobines, it is surprising that we know of no case of disease causing dramatic mortality in a population, though some deaths have been attributed to illness. Struhsaker (2010) describes a disease that causes ulcers on the face, scrotum, penis and perineum of red colobus in Kibale, which is suspected as the cause of the death for at least 10 of the 17 adult males in one group. At the Kanyawara site, this disease was first described in 1972 (Struhsaker 2010), but was not observed again until approximately 2012 (Chapman and Goldberg unpublished data). Recently there have been a number of viruses described in red colobus (Goldberg et al. 2008a; Goldberg et al. 2009; Lauck et al. 2011; Lauck et al. 2013a; Lauck et al. 2013b), but there is no indication of these viruses leading to acute mortality. Until data to the contrary are available, disease should not be considered as a major factor influencing colobine populations.

Conclusions

Despite attempts to better understand the factors affecting colobine population dynamics, empirical data on the effects of food quality and availability, competition for food resources, predation and disease remain limited. Given the extent of

deforestation and the occurrence of bushmeat hunting, it is imperative that we establish more protected areas that effectively restore critical habitats, as well as reducing deforestation and bushmeat hunting in general (Chapman et al., in press). However, our ability to do this is currently very limited. Food quality, particularly its protein-to-fibre ratio, warrants further research as a parameter that may limit colobine populations, but there are a number of reasons to doubt the generalizability of this model. The composition of forests (i.e. relative abundance of leguminous trees), and the food they contain, may also be a promising means to elucidate colobine population limits in Southeast Asia, but this does not generalize to Africa. There is no evidence that natural disasters occur with sufficient frequently to limit colobine numbers, particularly with their dietary flexibility. Given the difficulty of determining niche overlap and competition, no conclusion can be made regarding the role of interspecific competition in limiting colobine abundance. Predation of both African and Asian colobines occurs, and despite the high rate of predation by chimpanzees in some areas leading to declines in local populations of colobines, predation does not seem to be a general limiting factor. Finally, there is no evidence that disease limits colobine populations, despite its importance in some other monkeys and apes.

Interestingly, we have reached many of the same conclusions regarding factors influencing colobine populations as did Davies (1994) over 20 years ago, despite having added new data and additional examples to this important discussion. It seems most likely that colobines are limited by food availability, but the exact nature of that limitation remains unclear. It is interesting to ask why few advances have been made, but is clear that plenty of opportunities exist to conduct more thorough and detailed research into the question of what limits colobine populations. Areas that we view as especially promising are (1) the nutritional quality of colobine foods with respect to protein, fibre and other parameters like energy, minerals etc.; (2) the importance of disease (e.g. while disease may not cause direct mortality, it may decrease fitness and limit longevity); and finally, (3) the quantification of interspecific competition, such as the study conducted by Houle and colleagues (2006) on cercopithecines. This is especially important given that global deforestation rates in tropical regions are expected to rise as the need to feed the earth's growing population increasingly requires more land for agriculture.

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