

Do Food Availability, Parasitism, and Stress Have Synergistic Effects on Red Colobus Populations Living in Forest Fragments?

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ABSTRACT Identifying factors that influence animal density is a fundamental goal in ecology that has taken on new importance with the need to develop informed management plans. This is particularly the case for primates as the tropical forest that supports many species is being rapidly converted. We use a system of forest fragments adjacent to Kibale National Park, Uganda, to examine if food availability and parasite infections have synergistic effects on red colobus (*Piliocolobus tephrosceles*) abundance. Given that the size of primate populations can often respond slowly to environmental changes, we also examined how these factors influenced cortisol levels. To meet these objectives, we monitored gastrointestinal parasites, evaluated fecal cortisol levels, and determined changes in food availability by conducting

complete tree inventories in eight fragments in 2000 and 2003. Red colobus populations declined by an average of 21% among the fragments; however, population change ranged from a 25% increase to a 57% decline. The cumulative basal area of food trees declined by an average of 29.5%; however, forest change was highly variable (a 2% gain to a 71% decline). We found that nematode prevalence averaged 58% among fragments (range 29–83%). The change in colobus population size was correlated both with food availability and a number of indices of parasite infections. A path analysis suggests that change in food availability has a strong direct effect on population size, but it also has an indirect effect via parasite infections. *Am J Phys Anthropol* 131:525–534, 2006. © 2006 Wiley-Liss, Inc.

A fundamental goal in ecology is identifying factors determining animal population abundance (Boutin, 1990). The importance of this goal has increased with the need to develop informed management plans for endangered or threatened species. With respect to folivores, building on the pioneering work of Milton (1979), several researchers have indicated the importance of protein availability in determining folivore abundance, and several subsequent studies have found positive correlations between colobine biomass and the ratio of protein to fiber, both at local (Chapman and Chapman, 2002; Chapman et al., 2002a, 2004a; Ganzhorn, 2002) and regional scales (Oates et al., 1990; Davies, 1994). While this information will be useful in conservation planning, finding single factor explanations for complex biological phenomena, such as determinants of folivore abundance, is unlikely. Rather, long-term studies have highlighted the importance of multifactorial explanations. For example, based on a 68-month study of the effect of the parasitic bot fly (*Alouattomyia baeri*) on howler monkeys (*Alouatta palliata*), Milton (1996) concluded that the annual pattern of howler mortality results from a combination of effects, including age, physical condition,

and larval burden of the parasitized individual, which becomes critical when the population experiences dietary stress. Similarly, Gulland (1992) studied the interactions of Soay sheep and nematode parasites and demonstrated that at times of population crashes sheep were emaciated, had high nematode burdens, and showed signs of protein-energy malnutrition. In the field, sheep treated with antihelminthics had lower mortality rates, while

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experimentally infected sheep with high parasite loads, but fed nutritious diets, showed no sign of malnutrition.

It is possible that disease/parasitism and nutrition often interact to determine the abundance of wildlife populations. Helminthic and protozoal parasites can impact host survival and reproduction directly through pathological effects and indirectly by reducing host condition (Coop and Holmes, 1996; Murray et al., 1998). Severe parasitosis can lead to blood loss, tissue damage, spontaneous abortion, congenital malformations, and death (Collias and Southwick, 1952; Despommier et al., 1995). However, less severe infections are more common and they may compromise digestion or nutrient absorption, increase energy expenditure, and impair travel, feeding, predator escape, and competition for resources or mates (Hudson et al., 1992; Coop and Holmes, 1996). Some parasites extract significant amounts of nutrients from hosts, resulting in marked reduction in energy uptake (Moller et al., 1994), but others appear to cause little or no effect on host energetics (Munger and Karasov, 1989). Animal body condition and reproductive status can be compromised when parasites inflict substantial energetic costs (Hudson, 1986; Toque, 1993). However, parasites do not necessarily induce negative effects if hosts have adequate energy reserves or nutrient supplies concurrent with infection (Munger and Karasov, 1989; Gulland, 1992; Milton, 1996), suggesting that the outcome of host-parasite associations may be contingent on host nutritional status, as well as on the severity of infection.

Dietary stress may exacerbate the clinical consequences of parasitic infection through immunosuppression (Holmes, 1995; Milton, 1996). If so, then food shortages could result in higher parasite burden, which in turn could increase nutritional demands on the host and exacerbate the effects of food shortages. If this occurred, nutritional status and parasitism would have synergistic effects on the host, i.e., the individual effects of each factor would be amplified when co-occurring. The interactions between nutritional stress and parasitism have been examined in a number of laboratory studies (Keymer and Hiorns, 1986; Munger and Karasov, 1989) and a handful of field studies (Gulland, 1992; Toque, 1993; Murray et al., 1998), and they have led to speculation that vertebrate populations may be influenced by interactive effects of food shortage and parasitism (Keymer and Hiorns, 1986; Holmes, 1995; Murray et al., 1998).

One limitation of many previous studies exploring the potential for a synergism between nutritional status and parasite infections in wild populations is that researchers must monitor populations over considerable periods of time to repeatedly witness if changes in nutritional status and parasite infections are associated with changes in host population size. Here we attempt to circumvent this limitation in two ways. First, we examine a series of populations where food availability was thought to differ markedly (Onderdonk and Chapman, 2000; Chapman et al., 2004a). Anthropogenic fragmentation often produces isolated populations where food availability differs among fragments (Laurance and Bierregaard, 1997) and potentially harboring different parasite infections. This makes it possible to obtain the sample size of what can be considered independent populations to correlate population change to food availability and level of parasite infection.

Second, we explore the use of stress hormones to monitor the status of populations. Research on captive mammals and humans demonstrates that high and prolonged ele-

vated glucocorticoid levels (cortisol is one type of glucocorticoid) typically reduces survival and reproduction (Wasser et al., 1997; Creel, 2001; Creel et al., 2002; Bercovitch and Ziegler, 2002). Although data on fitness effects of elevated glucocorticoid levels in the wild are currently limited, the expectation from lab studies is that fitness will decrease as population level stressors become more severe or more prolonged (Boonstra and Singleton, 1993; Creel et al., 2002). Here we examine if a population's average cortisol level is correlated with the food available to the population or its parasite infections. If positive associations are found, it is reasonable to assume that populations with high cortisol levels are physiologically challenged, and in the long run, they will suffer reduced survival and reproduction. As well as considering a population's average cortisol level, we evaluate the degree of variation in cortisol levels. Here we assume that high variance in cortisol levels indicate that some individuals in the population are more stressed than others. With social primates, it is most likely that variation in cortisol levels will be a function of dominance, but unfortunately, it is not clear how cortisol will vary in association with dominance. Dominant individuals may have improved access to resources that could boost overall condition and immunocompetence (Abbott et al., 2003). Alternatively, increased levels of aggression associated with high rank may lead to higher levels of testosterone and stress, which could lead to greater susceptibility to parasite infections (Combes, 2001). Potentially reflecting these alternative possibilities, conflicting or ambiguous empirical patterns have been found to date between dominance and parasite infection levels in primates. For example, Hausfater and Watson (1976) documented that dominant yellow baboons (*Papio cynocephalus*) had higher outputs of helminth eggs. In contrast, Muller-Graf et al. (1996) found no association between dominance rank and indices of helminth infection in olive baboons (*P. anubis*), while Eley et al. (1989) have documented that lice were more common on low-ranking olive baboons.

Since 1995 we have been studying the colobus populations inhabiting a series of forest fragments outside of Kibale National Park, Uganda. These fragments are community owned, and each has experienced a different history of land use. This setting, along with knowledge of the population dynamics of the colobus in each fragment, offers a quasi-experimental setting, with each fragment being an independent population, since dispersal among fragments is rare. Therefore, it is possible to relate patterns of population change to food availability and disease profiles of these populations.

The purpose of this research was to use this setting to examine if food availability and parasite infections could have synergistic effects on red colobus (*Piliocolobus tephrosceles*) and influence their abundance. Given that primate population size can respond very slowly to even dramatic environmental change (Struhsaker, 1976), we wanted to evaluate how food availability and parasite infections influenced a more immediate measure of stress. Thus, we determined if food availability and parasite infections predicted the populations' fecal cortisol levels, and whether there were any indications that this index of stress was related to population change.

METHODS

Sites and samples

Since 1995 we have studied 19 forest fragments neighboring Kibale National Park (795 km²) in western

Uganda (Onderdonk and Chapman, 2000; Chapman et al., 2004a). As part of this program, we determined the population size of red colobus in 11 remaining fragments in May through November 2000 and again from May through July 2003. Unfortunately, some of these populations are currently very small, thus for analyses of population change we consider those eight fragments censused in 2000 and 2003 that had a reasonably sized red colobus populations in 2000 (average 17 individuals, range 7–24).

Kibale is a mid-altitude, moist-evergreen forest receiving 1712 mm of rainfall annually (1990–2004) during two rainy seasons (Chapman et al., 2004b). Prior to clearing for agriculture, there was likely continuous forest throughout the region. Now only small pockets of forest remain in areas unsuitable for agriculture. These fragments are community owned, thus they are degraded to varying degrees depending on the needs of the neighboring households (Naughton-Treves and Chapman, 2002). Around Kibale, people use land primarily for smallholder farming (54% of the area within 1 km) and human population density is ~ 272 individuals/km². Farms near Kibale average 1.4 hectare, of which on average 40% lies fallow (Naughton-Treves, 1998).

Forest fragments were originally selected if they had a clearly defined boundary, were isolated from other fragments or tracts of forest by ≥ 50 m, and were small enough to count all primate groups (Onderdonk and Chapman, 2000). To obtain reliable estimates of population size, observers often stayed with a group for up to 12 h and wait for members to make a coordinated movement across an opening in the canopy. Given our sampling effort and small fragment size, we believe that we obtained a complete census of all individuals. Even though fragments could be fairly close to one another, red colobus appeared to be very hesitant to move on the ground among fragments. During monthly sampling of one fragment over the last 13 years (Chapman et al., 1998) and over 330 h of behavioral observation, we never observed a group make a temporary visit to this fragment; however, a permanent move was seen when a distant fragment was largely deforested (Chapman et al., 2005).

Assessment of parasite community

From August 1999 to June 2004, we collected 634 fecal samples from red colobus in forest fragments (mean per fragment 79.4). Fecal samples were collected, stored individually in 10% formalin solution, and processed using concentration by sodium nitrate flotation and fecal sedimentation (Sloss et al., 1994). Eggs and larvae of parasites were counted and identified on the basis of egg color, shape, contents, and size. Coprocultures and necropsies were used to match parasite eggs to larvae for positive identification (Gillespie et al., 2005a,b).

The parasite infections were described in terms of prevalence of infection, richness, and multiple infections. Comparisons of parasite prevalence can be a useful indicator that parasites may be impacting host populations (i.e., population declines have been correlated to increased infection prevalence). Prevalence is the proportion of individuals sampled that are infected with a particular parasite. Since we could not individually recognize each animal in the population each year, we attempted to collect samples in a short period of time once each year and we tried to rotate among individuals so as not to repeatedly sample

the same individual. However, repeat samples likely occurred and thus this should be viewed as an index of prevalence. This is a concern since a small number of animals with consistently high infection levels and high richness could be over-represented in the sampling scheme, particularly since sick animals can defecate more than healthy individuals (see Muehlenbein, 2005 for a discussion of this issue). In a quantitative evaluation of this issue Huffman et al. (1997) contrasted incidences of infection based on the number of fecal samples obtained from chimpanzees (*Pan troglodytes*) from Mahale, Tanzania versus that based on the number of known individuals and documented that individual infection rates, the preferred unit of comparison, were statistically higher than rates based on all samples. The frequency of multiple-species infections (i.e., the proportion of a population with >1 species of parasite) can be another useful index, as multiple-species infections are associated with a greater potential for morbidity and mortality. Richness is the number of unique intestinal species documented from the host's fecal sample and an increase in richness could be indicative of greater morbidity. Parasite egg production is often highly variable and thus may not be indicative of actual infection intensity; however, it is frequently reported to describe infections (e.g., Gulland, 1992; Ezenwa, 2003). With *Trichuris* sp. from red colobus we typically obtain <10 eggs/g; however, for some groups at some times animals consistently have over 300 egg/g (all individuals in a group for an extended time). This suggests that this might be a useful index of parasite infection, but we suggest that the results be viewed critically and only be considered of interest if they are in concordance with other indices of parasite infection.

Assessment of stress—Cortisol

To evaluate fecal cortisol, 98 fecal samples (average 12.3 per fragment, range 8–24) were collected in 2003 (primarily June) from the eight fragments, and the age and sex of the animal was determined. As fecal steroid levels can vary along a number of dimensions, the conditions under which samples were collected were carefully defined. First, all samples were collected between 0800 and 1400 hrs to reduce variation that can be caused by diel variation in the excretion patterns of fecal steroids (Sousa and Ziegler, 1998). However, this is still a fairly long diurnal period, thus to examine diurnal variation in more detail, fecal samples were collected from four adult males and four adult females with infant, with each individual followed for one day (0800–1800 hrs), for a total of eight days of sampling within Kibale National Park. We documented that fecal cortisol levels did vary over the course of the day (1.9% increase per h) and that this pattern of variation was the same for all individuals (Wasserman and Chapman, unpublished data). If we compare levels from the earliest to the latest hour that samples were collected, there would be an 11.6% increase. Thus, in the analysis presented, the cortisol samples were adjusted to the most common time that samples were selected, even though there was no significant difference between fragments in the time of collection ($F = 0.1422$, $P = 0.207$).

Second, since cortisol levels increase with maturation (Bercovitch and Clarke, 1995), samples were collected only from adult animals. Third, because cortisol changes in association with pregnancy and it is not possible to determine when a female is in the early stages of preg-

nancy, samples were only collected from adult males and females with young infants. Finally, the lag time between a stress event (i.e., the appearance of steroids in the plasma) and appearance of steroids in the feces varies among species, but is typically between 12 h and 2 days (Schwarzenberger et al., 1996). Since the presence of observers may stress animals, samples were collected on the first day of observation, and then, at least a 7-day break was taken before any additional samples were taken.

We attempted to collect a single sample from all adult males and females with infant in each group that met our selection criteria (i.e., the group was large enough) in each of the eight fragments. This was done each day we visited a fragment, with collections typically made on 2–3 different days for each group. Upon defecation, samples were immediately placed in vials stored on ice. At the end of the day the samples were transferred to a -20°C freezer and stored until lab analyses. Fecal cortisol and metabolites were solubilized from a 0.5-g sample of fecal material using a 5.0 pH citrate buffer and 95% ethanol solution that was mixed for 21–27 h. After extraction, samples were placed in a centrifuge for 30 min. This supernatant (with solubilized hormones) was processed by passing 2 ml of supernatant through an Alltech maxi-clean filter cartridge. These cartridges were analyzed at the National Primate Research Center at the University of Wisconsin-Madison. The cartridges were washed with 1 ml of 20% methanol and the columns were eluted with 2 ml methanol. This methanol was dried, resuspended in 1 ml ethanol, and 50 μl was taken for the EIA (enzyme immunoassay). The assay followed the methods reported in Ziegler et al. (1995). These analyses provided data on the metabolites of cortisol found in the supernatant, validated the EIA, and resulted in a measure of the amount of cortisol and metabolites in each sample in nanogram per gram of dry feces. The dry weight of each sample was calculated in the field by drying to constant weight and calculating the percent water. Parallelism was demonstrated using serial dilution curves, with no significant difference between the sample pool and standards ($P > 0.05$). The accuracy of the procedure was $(125.27 \pm 3.18)\%$. To assess procedural variance we ran two pools and for the first the inter/intra-assay coefficient of variance was 19.8/5.1, while for the second it was 21.3/5.

Assessment of changes in food availability

To assess the changes in the food available in each of the fragments, we identified and measured diameter at breast height (DBH) of all trees greater than 10 cm DBH in 2000 and again in 2003. When trees were on extremely steep sides of the craters, their size was visually estimated (error in visual estimation = $\pm 3.8\%$). As colobus monkeys rarely feed in small trees (Gillespie and Chapman, 2001), this represents a nearly complete inventory of all major potential colobus food sources. Subsequently, trees were classified as important food trees if they were in the top five most frequently eaten species at any of the seven sites within Kibale forest or at one forest fragment. This is based on 3,355 h of observations (Chapman et al., 2002b). A number of studies support the use of DBH or basal area as an indicator of plant productivity (Catchpole and Wheeler, 1992; Chapman et al., 1992).

Analysis

Our overall objective was to determine if changes in the abundance of red colobus or population stress level (cortisol and variance in cortisol) in the fragments were related to changes in food availability or parasite infections. To meet this objective we index change in food availability by the change in the cumulative DBH of food trees available to the populations between 2000 and 2003 expressed as change in cm DBH/ha. However, to examine associations with parasite infections is not so straight forward, since there are a number of indices available to describe the infections. Thus, we first present correlations between population differences, cortisol level, variance in cortisol level, and descriptors of parasite infections. Subsequently, we conduct stepwise multiple regressions to determine which combination of the major descriptors of parasite infection best predicted the dependent variables. Since the number of fragments is small ($n = 8$) and since some authors have pointed out problems with stepwise multiple regressions (James and McCulloch, 1990; Bronikowski and Altmann, 1996), we also used the two independent variables with the highest Pearson correlation coefficients in a forced entry regression to predict the dependent variables. These regressions mirrored the results of the stepwise multiple regressions in indicating the most important predictor variable and thus are not reported. Since we had a priori predictions of how population change and cortisol would respond to changes in food availability and parasite infections, one-tailed tests are reported. Next, because many of the potential explanatory factors (i.e., indices of parasite infections) were auto-correlated, path analysis were used to determine the potential structuring of the relationships among variables.

For our purposes, path analysis is very useful since the path coefficients among the variables allow the determination of the magnitude of both direct and indirect effects among variables. In our study, we are particularly interested in the indirect effects of how changes in food supply influence population change through its impact on susceptibility to parasite infection. Path analysis begins with the construction of a path diagram showing the relationships among the variables in the system based on a priori knowledge of how the system operates (Kingsolver and Schemske, 1991). In our case this means that the diagram is based or rooted on changes in food availability, which can have a direct effect on population size, or an indirect effect on population size via parasite infections. In these analyses there are a number of independent variables measured with different units, but the path coefficients, or beta coefficients, are standardized regression coefficients that allow one to compare the relative effect on the dependent variable of each independent variable. Despite the advantages of path analysis, it should not be used to infer causation among variables (Shipley, 1999). Rather path analysis identifies correlations among variables, including both direct and indirect effects, and these represent possible targets of selections that can be further tested using an experimental approach (Kingsolver and Schemske, 1991). Since the number of fragments that still maintained large sizable colobus at the end of the study was few, and since there are many indices of parasite infections, in both the path analysis and the stepwise multiple regression, we considered only major indices of parasite infections (richness, prevalence of all nematodes,

TABLE 1. Descriptions of the density, tree community, cortisol, and gastrointestinal infections of the red colobus (*Ptilocolobus tephrosceles*) in a series of forest fragments neighboring Kibale National Park, Uganda

Fragment	CK Durama	Kiko II	Kiko III	Kiko IV	Kiko1	Lake Nyaherya	Lake Nkuruba	Rutoma
Fragment type	Valley + Hill	Valley	Valley	Valley	Valley	Crater lake	Crater lake	Hill side
Number of households	16	6	3	5	9	8	2	8
Activity in the fragment	B, G, L, W	C, W	W	W	L, W	C, L, W	W	G, W
Density 2003 (ind/ha)	2.30	2.6	8.24	11.67	2.10	0.65	3.28	7.50
% Change in density	25.00	-18.75	-41.67	-41.67	-27.78	-57.14	16.67	-25.00
Trees/hectare 2003	86	63	171	230	38	30	40	28
% Change in food DBH	-14.24	-58.91	-41.43	-24.08	-71.92	-12.18	2.89	-16.21
Stumps/hectare	45.75	8.40	221.76	174.17	56.45	15.00	1.00	337.50
Cortisol (ng/g)	139.23	386.68	445.12	230.66	165.68	144.10	245.85	356.03
Richness	0.49	0.88	1.29	0.667	0.91	0.44	0.294	0.4
Prevalence of Nematode	47.46	78.05	83.33	66.67	73.17	44.44	29.41	38.18
Prevalence of <i>Trichuris</i>	45.76	63.41	54.17	60.00	62.79	33.33	27.54	36.36
Prevalence of <i>Strongyloides füllebornii</i>	0	7.32	16.67	3.33	11.63	0	0	0
Prevalence of <i>Strongyloides stercalis</i>	0	0	12.5	0	0	0	0	0
Prevalence of <i>Oesophagostomum</i>	1.69	7.32	16.67	3.33	4.65	11.11	0.27	0.00
Prevalence of strongyle nematode	1.69	4.88	16.67	0.00	11.63	0	0	3.64
<i>Trichuris</i> egg/g	2.02	9.2	3.8	2.5	8.84	0.44	1.4	3.3
All Nematodes egg/g	2.05	9.65	9.68	8.42	2.57	1.36	0.56	3.36
Proportion with Multiple Infections	1.69	9.76	33.33	0	23.26	0	0	1.82

For Activity type, B, beer; G, gin; C, charcoal; L, livestock, and W, woodlot.

egg/g of all nematodes) and did not consider individual parasite indices (e.g., prevalence of *Oesophagostomum* sp.). We also limit our path analyses to simple models involving three variables and report both significant and nonsignificant path coefficients, recognizing that a comparison of the size of the coefficient is indicative of the size of an effect among variables.

RESULTS

Red colobus population change in forest fragments

Of the original 19 fragments surveyed in 1995, 11 supported red colobus in 2000 and nine in 2003. None of the original fragments occupied by red colobus were cleared in the 8 years between censuses. In 2000 we counted 127 red colobus in the eight fragments we considered, while in 2003, 102 animals were seen in those same fragments. In the 2000 census, 55 adult female red colobus were counted and the ratio of infants to adult females was 0.31. In the 2003 census, 54 adult females were counted and the ratio of infants to adult females was 0.19. The age/sex class that declined the most was the subadult category and there were 4 times fewer subadults in 2003 than there were in 2000. Among the eight fragments monitored in 2000 and 2003, populations declined at an average of 22%; however, population change over this period was highly variable and ranged from an increase of 25% to a decline of 57%. The change in red colobus density (mean change = 0.71 individuals/hectare, density range = 8.3–9.2 individuals/hectare, $n = 8$ fragments) was not correlated to the either size of the fragment, the number of households using it, or its distance to either Kibale or the nearest fragment ($P > 0.272$ in all cases, $n = 8$).

Changes in forest attributes

In all fragments we found evidence of forest clearing; however, the extent of clearing was extremely variable. The average size of the fragments containing red colobus was 4.4 hectare ($n = 8$ measured in 2000). In 2000 there were on average 99 trees/hectare (range 27–259 trees/hectare), while in 2003 there were 86 trees/hectare (range 30–230 trees/hectare). The basal area of trees in the fragments averaged 9002 m² in 2000 (range 1,981–39,012 m²) and 5,293 m² (range 1,772–28,397 m²) in 2003, and the cumulative basal area of food trees was 915 m² in 2000 (range 317–2,430 m²) and 535 m² (42–2,387 m²) in 2003. Thus, on average the basal area of food trees declined by 29.5% over the 3 years; however, forest change was highly variable. Lake Nkuruba, the site of a community-based conservation project, exhibited a 2% gain in food tree basal area, which is comparable to rates of growth of trees in undisturbed forest in the region (Chapman and Chapman, 2004). In contrast, forest clearing led to a 71% decline in food tree basal area in a fragment within a tea plantation. In 2000, exotic species, primarily *Eucalyptus* sp. constituted 16% of the food tree basal area, while in 2003 this value had risen to 28%. There was little change in tree richness between time periods (2000 = 11.5 species/hectare, 2003 = 11.6 species/hectare).

Parasite community

The parasite communities described from the 634 red colobus fecal samples collected from the eight forest fragments between August 1999 and June 2004 included the following nematodes: *Trichuris* sp. (Superfamily Trichuroidea), *Oesophagostomum* sp. (Superfamily Strongyloidea), *Strongyloides füllebornii*, *S. stercoralis* (Superfamily Rhabditoidea), and an unidentified strongyle. We also identified three protozoans, *Entamoeba coli*, *E. histolytica/dispar*,

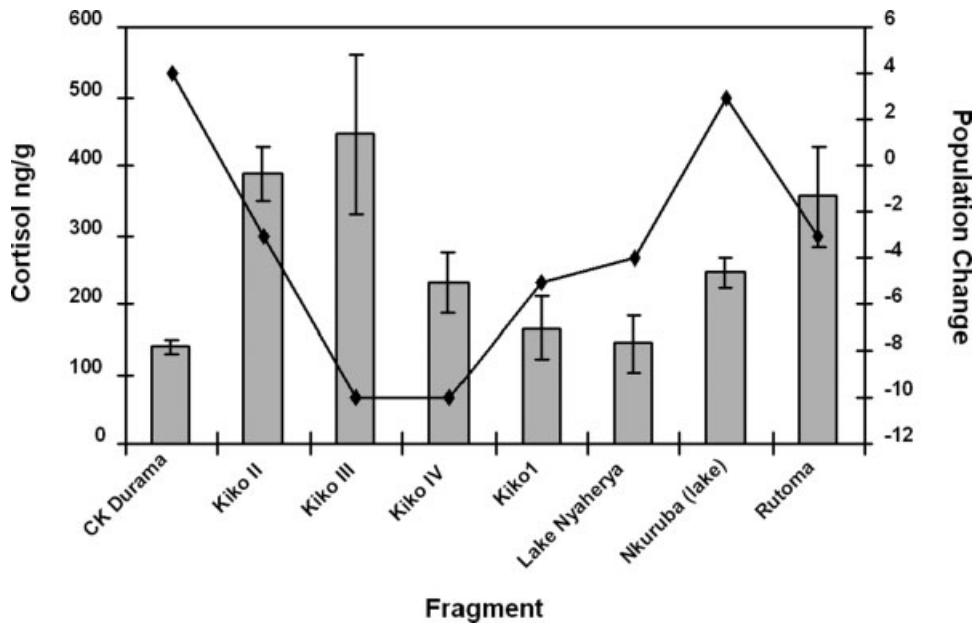


Fig. 1. The cortisol levels (\pm SE) measured from red colobus monkeys (*Piliocolobus tephrosceles*) in a series of forest fragments neighboring Kibale National Park, Uganda and the corresponding population change in that fragment.

and *Giardia* sp. (likely *G. lamblia*). Additionally, in one individual, an *Ascaris* sp. egg (Superfamily Ascarioidea) was found. However, because of the difficulty of quantifying protozoan infections and the small sample size for the *Ascaris* sp., these parasites are not considered further.

On average, three of the five major parasite species were found in any one fragment, but this ranged from 1 to 5 species. The number of species found was independent of the number of samples collected (Spearman rank correlation $r_{sp} = -0.160$, $P = 0.706$). The average parasite richness of all individuals averaged 0.67 species (range 0.40–1.29 species), while the richness in infected individuals averaged 1.14 (range 1–1.55; Table 1). The percentage of the population in each fragment that had multiple infections average 8.7% (range 0–33%). Nematode prevalence averaged 58% across the fragments (range 29–83%). This was strongly influenced by the abundance of *Trichuris* sp., which had an average prevalence of 48% (range 28–63%). Mean prevalence of *Oesophagostomum* sp. was 5.6% (range 0–17%). *S. fulleborni* prevalence averaged 4.9% (range 0–17%). The prevalence of *S. stercoralis* was the lowest of all nematodes examined, averaging 1.6% (range 0–13%). Mean prevalence of the unidentified strongyle was 4.8% (range 0–17%). The average number of parasite egg/g averaged 4.71 among fragments (range 0.56–9.68 eggs/g). These values were heavily influenced by the abundance of *Trichuris* sp., which on average had 3.94 eggs/g among fragments (0.44–8.84 egg/g; Table 1).

Gillespie and Chapman (2006) have previously documented elevated parasite infections in primate in forest fragments compared to groups in the main forest. Analyzing the smaller subset of fragments here documents similar differences to those reported earlier (e.g., nematode prevalence: forest in Kibale National Park = 41.73, in fragments 57.59; *Trichuris* sp. prevalence 40.77, 47.92, *Oesophagostomum* prevalence 0.96, 5.63, nematode egg/g 2.51, 4.71; proportion of multiple infections 3.54, 8.73).

Cortisol levels

Cortisol levels averaged 264 ng/g among fragments, but ranged from 140 to 446 ng/g. The cortisol levels for

the fragments were not correlated with the number of samples collected ($r = -0.160$, $P = 0.704$). The fragment with the least cortisol in the samples was 2.7 times less than the fragment with the highest cortisol level (see Fig. 1). Further, the fragment with the most variable cortisol levels was 4.3 times more variable than the least variable fragment. The estimate of the variance in cortisol level within a population was not related to the number of samples analyzed for that population ($r = -0.286$, $P = 0.197$).

The cortisol levels for groups in the intact forest of Kibale National Park were ~ 3.5 times lower than the average value for the forest fragments when comparisons are made to the same month of collection or the same month in the subsequent year (Kibale Group 1 June 2003 = 76.4 ng/g, range 44.6–154.4 ng/g; Group 1 June 2004 = 82.9 ng/g, range 42.9–153.2 ng/g; Group 2 June 2004 = 66.3 ng/g, range 31.0 to 145.4 ng/g). Animals from the continuous forest seldom had values as high as the lowest value from the fragments.

Population change and stress in relation to food availability and parasitism

An increased rate of forest loss (i.e., decline in cumulative DBH of food trees) was related to a decrease in population size (Table 2), but it also was associated with an increase in indices of parasitic infection, and an increase in parasitism also corresponded to a decline in population size. With respect to cortisol, the picture is not as clear. An increase in deforestation was only marginally related to elevated cortisol levels ($P = 0.055$; Table 2). However, an increase in cortisol was related to an increase in some of the indices of parasite infections. There was no significant correlation between population change and cortisol levels.

In stepwise multiple regressions predicting population change or variance in cortisol, only changes in food availability entered the stepwise regression (population change $r^2 = 0.685$, $P = 0.011$; variance in cortisol $r^2 = 0.664$, $P = 0.014$). When attempting to predict cortisol

TABLE 2. Correlations between population change, fecal cortisol level, variance in fecal cortisol, and food availability in red colobus in a series of forest fragments neighboring Kibale National Park, Uganda

Predictor	Population change		Cortisol		Variance in cortisol	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
<i>Major variable</i>						
Change in food availability	0.827	0.006	-0.599	0.055	-0.801	0.008
Parasite richness	-0.668	0.035	0.530	0.088	0.634	0.046
Prevalence of nematodes	-0.689	0.029	0.414	0.154	0.498	0.105
Nematode egg/g	-0.692	0.029	0.713	0.024	0.649	0.048
Proportion of multiple infections	-0.505	0.101	0.464	0.123	0.626	0.048
<i>Minor variable</i>						
Prevalence <i>Trichuris</i> sp.	-0.548	0.080	0.212	0.308	0.307	0.230
Prevalence <i>Oesophagostomum</i> sp.	-0.593	0.061	0.373	0.180	0.412	0.155
Prevalence <i>Strongyloides fuelleborni</i>	-0.621	0.050	0.500	0.103	0.629	0.047
Prevalence <i>S. stercoralis</i>	-0.510	0.099	0.621	0.050	0.669	0.035
Prevalence unidentified strongyle	-0.488	0.110	0.509	0.099	0.699	0.027
Egg/g <i>Trichuris</i> sp.	-0.201	0.317	0.305	0.231	0.365	0.187

Pearson correlation coefficient and probability levels, with significant values in italic. Egg/g is only presented for *Trichuris* sp. since for the other species it was rare to find more than 1 egg per sample.

TABLE 3. Path coefficients of changes in food availability and indices of parasitism on changes in red colobus population size, cortisol level, and variance in cortisol level in the red colobus (*Ptilocolobus tephrosceles*) populations inhabiting a series of forest fragments adjacent to Kibale National Park, Uganda

<i>Population Change</i>			
1st model	Richness	Pop change	Indirect path
Food availability	-0.609	0.668	0.159
Richness	-	-0.262	
2nd model	Prevalence	Pop change	Indirect path
Food availability	-0.575	0.644	0.183
Prevalence	-	-0.319	
3rd model	Egg/g	Pop change	Indirect path
Food availability	-0.710	0.677	0.150
Egg/g	-	-0.211	
<i>Cortisol</i>			
1st model	Richness	Cortisol	Indirect path
Food availability	-0.537	-0.433	0.149
Richness	-	0.281	
2nd model	Prevalence	Cortisol	Indirect path
Food availability	-0.537	-0.499	0.071
Prevalence	-	0.133	
3rd model	Egg/g	Cortisol	Indirect path
Food availability	-0.685	-0.230	0.352
Egg/g	-	0.513	
<i>Variance in Cortisol</i>			
1st Model	Richness	Variance in cortisol	Indirect path
Food availability	-0.573	-0.690	0.203
Richness	-	0.219	
2nd model	Prevalence	Variance in cortisol	Indirect path
Food availability	-0.537	-0.729	0.078
Prevalence	-	0.135	
3rd model	Egg/g	Variance in cortisol	Indirect path
Food availability	-0.685	-0.642	0.126
Egg/g	-	-0.230	

Pathways for the parasite indices are presented in Figure 1. Significant coefficients are in italic.

level, only the egg/g of all nematodes entered the equation ($r^2 = 0.507, P = 0.0487$).

We produced simple path analyses that considered each major index of parasite infection separately along with food availability (indexed as the loss in food trees (cm DBH/ha)) to predict population change (Table 3, Fig. 2).

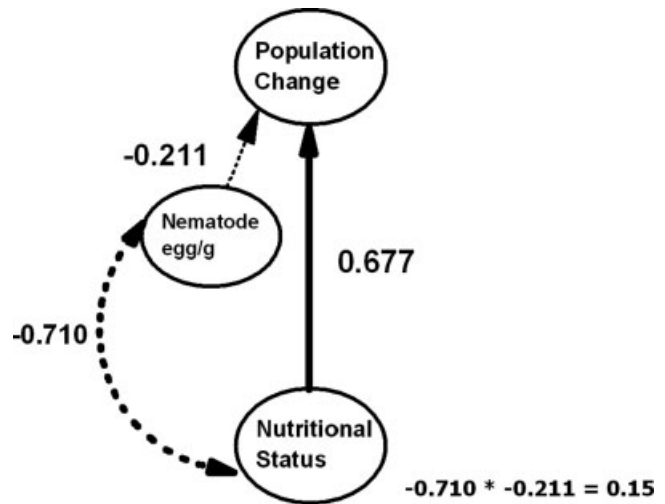


Fig. 2. An example, path analysis of factors predicted to affect the change in population size of red colobus monkeys (*Ptilocolobus tephrosceles*) in a series of forest fragments neighboring Kibale National Park, Uganda. Positive effects are indicated by solid lines and negative effects by dashed lines. Double headed arrows indicate positive relationships between predictor variables. The width of the arrow indicates the magnitude of the standardized path coefficients. Significant pathways and path coefficients are shown in Table 2, which also presents the same information with other predictors of population change, cortisol, and variance in cortisol.

Each of these analyses indicated that reduced food availability had a direct effect on population size leading to decline (Table 3) and in all cases the path coefficient was relatively large (mean = 0.663). Reduced food availability also had an indirect effect on population size through its influence on parasite infections. Here reduced food availability had an initial fairly strong effect on the indices of parasitism considered (mean = 0.631), which subsequently had weaker and negative effects on population size (mean = -0.264). As an example, while the direct effect of changes in food availability on population change is relatively large (0.677), as is the indirect effect of changes in food availability on nematode eggs/g (-0.710), the effect of changes in nematode eggs/g on population change is rela-

tively small (mean = -0.211). Thus, the total indirect effects are relatively small ($-0.710 \times -0.210 = 0.15$; Fig. 2) compared to the direct effect (0.677).

Including cortisol or the variance in cortisol in such three variable path analyses similarly suggests that reduced food availability has a large direct effect, but a small indirect effect, with one exception. In a three variable path (food availability, nematode load, and cortisol), the indirect path involving food availability and nematode load was stronger (path coefficient = 0.352) than the direct path (path coefficient = -0.230).

DISCUSSION

We found support for our prediction that there would be positive associations between population change, loss of food resources, and parasitic infections. Red colobus abundance declined with the loss of food trees, indicating that the availability of food resources is a major determinant of colobus population size. This finding is counter to the claim that folivore food resources are superabundant and evenly dispersed, and thus within-group scramble competition is weak or absent among folivorous primates (Wrangham, 1980; Isbell, 1991).

Population declines were also negatively associated with a number of the indices of parasite infection. This may reflect the direct negative influence of these gastrointestinal parasites, or, as is suggested by the path analysis that these parasites are taking advantage of a decline in the animal's immune system that is associated with poor nutrition. Several of the parasites infecting colobus in the Kibale region have the capacity to cause substantial pathology at high prevalence. Heavy infections of *Oesophogostomum* sp. and *Strongyloides* sp. are associated with mucosal inflammation, ulceration, dysentery, weight loss, and death. Even moderate infections of *Oesophogostomum* sp. have proven clinically important in stressed captive primates (Crestian and Crespeau, 1975). However, other parasites, like *Trichuris* sp., are typically asymptomatic and may not affect demography. Despite the potential of some parasites to cause pathology, the path analysis suggests that the direct effect of loss of food resources is ~ 4 times greater than the indirect effects of increased parasitism. It is possible that the effect of parasites might have been stronger, since by sampling throughout the period we could be sampling those animals left in fragments that are most fit and are able to survive under the parasite and nutrient conditions of the fragmented forest. Evidence from one fragment monitored over 5 years following a marked change in density suggests that as populations decline parasite infections remain high. Following the clearing of a forest fragment supporting red colobus and black-and-white colobus (*Colobus guereza*), animals moved into a neighboring fragment that we had been monitoring for a number of years and for which we were routinely monitoring parasite infections (Chapman et al., 2005). The immigration of animals into the fragment resulted in the colobus populations more than doubling and colobus density becoming almost twice that found in Kibale. In both colobus species the prevalence of *Trichuris* sp. increased. Over the next 5 years the prevalence and intensity of infection of *Trichuris* sp. in red colobus declined and their population numbers slowly increased. In contrast, the prevalence and intensity of infection of *Trichuris* sp. increased in black-and-white colobus and remained high following the immigration and their population size

declined. The challenge of applying this information to conservation is to connect the patterns we have documented to the reproductive success of individuals that vary in their severity of parasite infection (i.e., quantifying a change in parasitism with a change in fitness). An experimental approach that reduces parasite infections would be most revealing.

Cortisol was not related to population change, but the number of nematode egg/g found in their feces was positively associated with cortisol, and it was marginally related to other indices of parasite infections. There are a number of plausible explanations for the lack of association between cortisol level and population change. We used methodologies that would minimize variance that was unrelated to ecological factors (e.g., time of the day, age, reproductive condition); however, we could not control for social factors that could stress animals. Future studies should consider partitioning the variance in cortisol levels between ecological and social stressors. Interestingly, there was a weak association between the variance in a population's cortisol level and population change, with populations with more variable cortisol levels declining the most. Furthermore, the variance in cortisol was related to a number of indices of parasite infections. These findings highlight the importance of examining cortisol levels at an individual level, as well as at the population level, to understand how it varies with social factors and if these social factors are influenced by changes in ecological conditions. For example, dominant individuals may have improved access to resources that could boost overall condition and immunocompetence, or high rank may lead to increased need to assert dominance in ecologically stressful times, more fights, and higher levels of stress (Combes, 2001; Abbott et al., 2003). The lack of association between cortisol level and population decline may also reflect that some of our measurements were from populations that were only experiencing stress on the short term (e.g., short-term food shortage), while cortisol would have to be chronically elevated to high proportions to be responsible for a decline in population size. Thus, evaluation of cortisol levels in these populations over an annual cycle may illustrate a stronger association between stress and population change. Furthermore, there is the need to critically evaluate methods of evaluating cortisol to address conservation questions such as the one being addressed here. Some animals naturally have higher cortisol levels than others (Muehlenbein, in press), and cortisol can vary along a number of dimensions (e.g., positive as well as negative emotions; Pollard, 1995), group size (Pride, 2005)). Thus, at this time it is premature to make an evaluation of the use of cortisol to address such conservation issues and it is clear that the academic community needs to evaluate sources of variation in cortisol levels so that these can be controlled for in further applications of this tool.

Our findings support suggestions that nutritional status interacts with the host immune response and leads to a synergistic relationship between food availability and parasites to influence population change (Gulland, 1992; Holmes, 1995; Murray et al., 1998), but suggest that the direct effect of food availability has the strongest influence. Previous research examining population cycles has suggested the potential for such synergy at periods of peak density in the cycle, since at these times animals often face food shortages (Keymer and Dobson, 1987; Murray et al., 1996, 1998). But it also seems possi-

ble that this synergy operates in non-cycling species and not necessarily during periods of peak density, but when density is high relative to food availability. The situation we examined was an artificial one created by human habitat modifications where food resources were removed rapidly. Thus, the importance of the interaction of nutritional status and parasitism on population size in more natural systems needs to be examined. However, based on our past studies of variability in food availability for folivores (temporal and spatial; (Chapman et al., 2004b), along with the findings here in forest fragments where reduced food availability had the strongest influence on population change, it is likely that this synergistic relationship is critical in the population dynamics of red colobus in both human modified and unmodified habitats.

Understanding the ecological determinants of animal abundance has been a central question in the field of ecology since its inception. However, this issue has taken on new importance given the current rate of anthropogenic disturbance, the subsequent decline in many wildlife species, and the need to construct informed management plans. With respect to primates, these theoretical issues are critical because the tropical forests they occupy are undergoing rapid anthropogenic transformation. Cumulatively, countries with primate populations are losing ~125,000 km² of forest annually (Chapman and Peres, 2001). Other populations are affected by forest degradation (logging and fire) and hunting. Based on patterns of rural development and land conversion, we expected a decline in population size of red colobus living in unprotected fragments and this expectation was borne out by the surveys. These findings suggest a low conservation value for small unprotected forest fragments that provide communal resources. It is likely that most of these fragments will be destroyed and the colobus populations they support lost within this decade. However, the rate of conversion is highly variable depending on the needs of local land owners. It was this pattern of variability that allowed us to examine the interactive effects of food availability and parasitism on red colobus abundance. Examining this variability suggested that the loss of food trees associated with people using forests strongly affects colobus and leads to population declines. However, forest conversion also appeared to affect the colobus populations through its effect on parasitic infections. Since we have previously demonstrated that human modifications to landscapes can alter interactions between parasites and hosts (i.e., selective logging; (Gillespie et al., 2005a), this raises the intriguing question of what types of anthropogenic disturbances will lead to disease playing a more significant role in determining primate population size. In the future, between-site comparisons should be chosen carefully to explore the modifying effects of specific anthropogenic disturbances (e.g., forest fragmentation with or without elevated rates of human contact); because the focus has now shifted from *whether* anthropogenic habitat change alters primate-disease interactions to *how* anthropogenic change alters primate-disease interactions.

CONCLUSIONS

Identifying factors that influence primate density is critical in the development of informed conservation plans; however, there are few general models explaining variation in abundance. Here we studied a series of forest fragments outside of Kibale National Park, Uganda

to examine if food availability and parasite infections could have synergistic effects on red colobus (*Ptilocolobus tephrosceles*) abundance. Given that primate population size can respond very slowly to even dramatic environmental change, we also quantified fecal cortisol levels. Evidence suggests that a decline in food availability has a direct and negative effect on colobus population size, as well as an indirect effect of parasite infections, which in turn negatively impacts colobus abundance. The use of cortisol to monitor population status was ambiguous as it was only marginally related to declines in food availability, related to only some indices of parasite infections and not related to population change. Thus, at this time it is premature to make an evaluation of the use of cortisol to address such conservation issues using the approaches applied here.

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