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EFFECTS OF RAINFALL, HOST DEMOGRAPHY, AND MUSTH ON STRONGYLE FECAL EGG COUNTS IN AFRICAN ELEPHANTS (*LOXODONTA AFRICANA*) IN NAMIBIA

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ABSTRACT: Wild African elephants (*Loxodonta africana*) are commonly infected with intestinal strongyle parasites. Our objective was to determine baseline fecal strongyle egg counts for elephants in the northeast region of Etosha National Park, Namibia and determine if these numbers were affected by annual rainfall, elephant demography (age of individuals and composition of groups), and hormonal state of males. We found that matriarchal family group members have significantly higher fecal egg counts than male elephants (bulls). Among family group members, strongyle egg counts increased with age, whereas among bulls, strongyle egg counts decreased with age. Years of higher rainfall were correlated with decreased numbers of strongyle eggs among bulls. Finally, bulls were not affected by their physiologic (hormonal) status (musth vs. nonmusth). These results suggest that infection by strongyle parasites in Namibian African elephants is a dynamic process affected by intrinsic and extrinsic factors including host demography and rainfall.

Key words: African elephant, Etosha National Park, intestinal parasites, *Loxodonta africana*, Namibia, strongyle nematodes.

INTRODUCTION

Parasite studies of numerous free-ranging wildlife species have demonstrated that intrinsic and extrinsic factors such as environmental conditions, population density, and animal age can all affect intestinal parasite load as determined through parasite fecal egg counts (Krecek et al., 1989; Gulland, 1995; Masangane et al., 2004). In captive Asian elephants (*Elephas maximus*; Gaur et al., 1979; Suresh et al., 2001) and wild African elephants (*Loxodonta africana*; Kinsella et al., 2004; Jost et al., 2005), a wide variety of nematodes and protozoa have been described, but there are few studies evaluating the factors affecting parasite loads in elephants.

Within the phylum Nematoda, members of the superfamily Strongyloidea (strongyles) have been consistently observed in wild African elephants, with the genera *Choniangium, Decrusia,* and *Equinurbia* classified as large strongyles, and *Khalilia, Murshidia,* and *Quilonia* as small strongyles (Condy, 1973; Fowler and Mikota, 2006). Despite a lack of published information on the life cycle of the strongyle species infecting elephants, their biology is presumed to be similar to that described in horses and domestic livestock (Soulsby, 1982; Fowler, 2001).

We studied the relationships between African elephant hosts and their strongyle parasites in the context of several host and environmental factors in the semiarid savanna of Etosha National Park, Namibia. Specifically, we characterized the principal genera of strongyles infecting African elephants in this region and investigated the influence of demographics (host age, composition of groups),

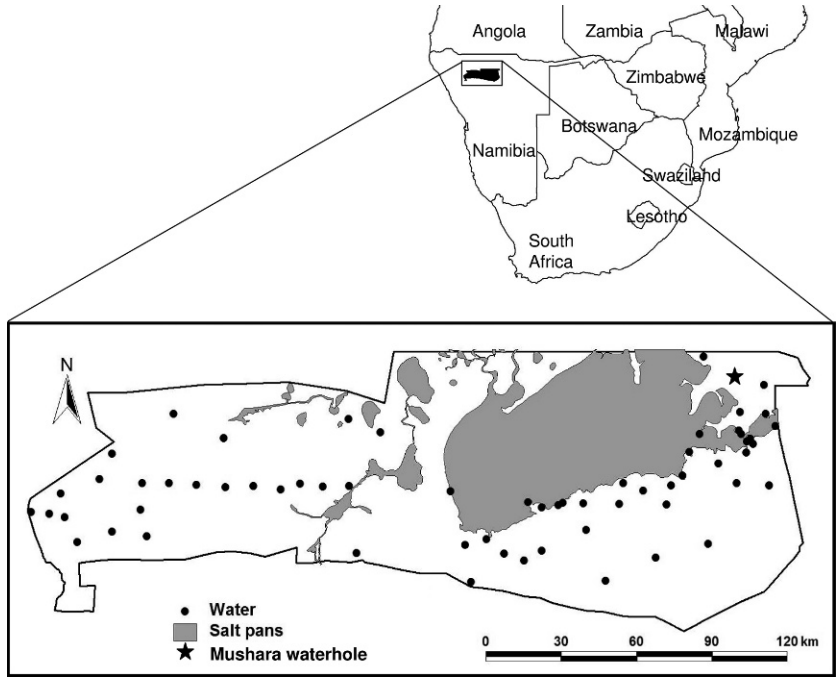

FIGURE 1. Map showing the Mushara Water Hole in the northeastern corner of Etosha National Park, Namibia (star), where studies of African elephants (*Loxodonta africana*) were conducted 2007–2009.

hormonal state of bulls (musth vs. nonmusth), and rainfall on the number of strongyle eggs per gram (EPG) of feces.

We hypothesized that rainfall, age, group composition, and musth would all have an influence on strongyle EPG. We expected that the strongyle EPG in wet years would be lower than in dry years because of better access to resources. Because older elephants tend to be more dominant (Poole, 1989a) and may have access to the highest-quality food, we hypothesized that adult elephants have lower EPG than younger elephants. Since bulls live in a less dense society than family group members (Buss, 1961), they may have decreased exposure to parasites compared with those in family groups. We therefore hypothesized that bulls would have lower EPG than family group members. Finally, because of the physiologic demands of the state of musth, we hypothesized that EPG in musth bulls would be greater than in nonmusth bulls. Bulls in musth require an increased energy output to maintain the state of musth (Poole 1999), and therefore may have a decreased ability to fight off parasitic infection.

MATERIALS AND METHODS

Study site

Field studies were conducted at Mushara Water Hole in Etosha National Park, Namibia (Fig. 1) for approximately 2 mo each year during the dry seasons of 2007–2009. Elephant observations were made from a multistory tower base camp within 80 m of the water source. The habitat in this region is considered sandveld; the major woody plant species are *Terminalia prunioides, Terminalia sericea, Croton menyhartii, Lonchocarpus nelsii, Grewia flava, Combretum collinum, Bauhinia macrantha,* and *Ochna pulchra* (Le Roux et al., 1988). During the dry season, available water in this region is limited to a few water holes, the closest to Mushara being 10 km (Fig. 1).

Etosha National Park experiences a wet season (November–April) and a dry season (May–October). All observations were made at the height of the dry season (June–July) from

TABLE 1. Average shoulder heights for bulls and matriarchal family group members corresponding with age range estimates (Kinzley et al., 2010) for African elephants (*Loxodonta africana*) in Etosha National Park, Namibia, 2007–2009.

Size[a]	Average bull shoulder height (m)	Corresponding age of bulls (yr)	Average family group member shoulder height (m)	Corresponding age of family members (yr)
One-quarter	2.70	≤14	1.92	≤6
One-half	2.90	15–24	2.04	7–12
Three-quarter	3.07	25–34	2.35	13–19
Full	3.14	≥35	2.41	≥20

[a] See methods for explanation of sizing.

2007–2009, but the year of observation was categorized as a "dry year" or "wet year" on the basis of the annual rainfall measured at the weather station in Namutoni, the closest tourist center to Mushara, during the previous wet season. The long-term average annual rainfall in Namutoni is 436 mm (de Beer et al., 2006). Fecal egg count data were analyzed during a relatively dry year, 2007 (399 mm of rain), and in relatively wet years, 2008 (600 mm of rain) and 2009 (650 mm; Etosha National Park rain data archive). This variation in annual rainfall allowed us to analyze the impact of rainfall on parasite load in elephants.

Elephant group composition and age

Elephants were categorized as being either a member of a family group (composed of a matriarch and her close female relatives and offspring) or a bull (a sexually mature male that tends to live in association with other bulls, with occasional time spent with females) to assess whether there is an impact of group composition on strongyle EPG. To determine the impact of age on strongyle EPG, elephants were grouped into age classes. Elephants are sexually dimorphic and continue to grow throughout their lives (Laws, 1966), but reliable methods have been developed to correlate elephant size with age, including shoulder height (Poole, 1999), hind foot length, and tooth measurements (Laws, 1966; Western et al., 1983).

Elephants were separated into four broad size categories on the basis of shoulder height (Table 1), which was used as an index of age, with the smallest (one-quarter size) elephants categorized as the youngest, and the largest (full size) elephants the oldest. Because of sexually dimorphic characteristics in elephants' size and weight, the scales used for family group members and bulls are different. A one-quarter-size bull that has recently left its matriarchal family group is slightly larger than a full-size matriarchal family group member (≤14 yr). In contrast, a one-quarter-size family member is a young elephant that has not left its family group (≤6 yr).

Shoulder height was measured on all elephants included in this study using a Trupulse™ 200 Laser Technology laser altimeter at a fixed distance (80 m) and location (the source of fresh water) as well as shoulder position (perpendicular to the observation tower). These data were then compared for accuracy against a fixed object positioned at the same spot with incremental measurements taped onto the object and visible from measurement distance. Relative height was used to categorize elephants when exact heights could not be measured.

Bull elephant identification

Bull elephants were identified on the basis of individual differences in their ear characteristics, tusks, tails, and penises, as well as overall size. These differences are recorded in an ongoing photo-identification database that has been compiled since 2005.

Elephant physiologic state

Musth is a physiologic state of sexual maturity in bulls manifested by observable characteristics including urine dribbling, temporal gland secretions, and heightened sexual and aggressive activity (Poole, 1999; Ganswindt et al., 2005). These physical and behavioral characteristics are easy to document visually, but because studies have shown that urine dribbling is highly correlated with the height of musth and peak testosterone levels (Ganswindt et al., 2005), we used this measure in our studies as the main criterion for identifying bulls in musth. Within the three-quarter- and full-size bulls, some bulls enter musth, whereas younger bulls are rarely observed in musth (Poole, 1989b). Therefore, only the three-quarter- and full-size bulls were

evaluated for musth status to determine whether this physiologic state affects parasite loads.

Collection of feces

Feces deposited by individually identified elephants congregating around the water hole were mapped using a grid system and collected after the elephants left the area. Elephants were observed and identified while defecating, and the fecal samples were collected within 2 hr of defecation. Because fecal egg counts are based on the wet weight of feces, and sun exposure could dry out the fecal samples, moist fecal samples were collected from the inside of each bolus. The average elephant defecation (event) consists of three to six boluses. Multiple subsamples (two to three per bolus, weighing approximately 10 g each) were collected from each fecal event and mixed together to obtain a more representative sample from each elephant.

Fecal samples were collected from 189 individually identified elephants during our study and examined for parasite eggs. The estimates of EPG for individual elephants that were observed more than once in a season were averaged to minimize bias due to individual sampling variation. Of the 189 individuals sampled, 11 bulls were repeated twice, four bulls were repeated three times, and 16 bulls were repeated more than four times (Table 2); no family group members were repeated because of a lack of individual identification. From June to August 2007, we sampled only bulls (one-quarter size and larger), collecting a total of 28 fecal samples. From June to July 2008 and 2009, we sampled elephants of all ages and group types. In 2008, we sampled 48 bulls and 38 elephants of mixed ages and genders from family groups. In 2009, we sampled 43 bulls and 32 elephants from family groups.

Strongyle egg identification and quantification

Feces were processed according to Gibbons et al. (2004). Briefly, 8 g of fecal matter were mixed with 112 ml of supersaturated salt (NaCl) solution and poured through a tea strainer to remove large plant debris. Two aliquots of 0.15 ml of homogenized filtrate were placed into separate sampling chambers of the McMaster slide for 5 min before analysis to allow strongyle eggs to float and contact the upper surface of the slide. Parasite eggs with typical features of the strongyle family (Fig. 2) were counted at 10× magnification with a Fisher model 12-561-4B Micromaster II binocular bright-field microscope. Eggs per gram of feces were calculated using a standard formula on the basis of the known weight of feces (8 g), the flotation fluid used (112 ml), and the capacity of the chambers (0.30 ml):

$$[(\text{countchamber 1})+(\text{countchamber 2})] \times 50 = \text{EPG}.$$

Larval culture and identification

Forty-four fecal samples from a range of elephant ages and genders (23 bulls, of which three were in musth, and 21 family group members) were collected in 2009 for larval culture and identification. Eight grams of feces were mixed with 2 g of vermiculite and placed in a small plastic cup. Water was added until the mixture was damp. The cup was covered with plastic wrap and incubated on a bench top for 14 days to recover infective L_3 larvae.

Larvae were recovered using the Baermann technique. A hollow-stemmed disposable champagne glass was filled with warm water to within 1 cm of the rim. The cultured fecal samples were placed in two layers of cheesecloth, secured with a rubber band, placed in the glass, and covered with additional warm water. Overnight, the larvae in the feces migrated out through the cheesecloth into the hollow stem of the champagne glass, and a plastic pipette was used to collect 0.5 ml of sediment from the bottom of the stem, which was then preserved in an Eppendorf tube in 1.5 ml of 100% ethanol. Two identical aliquots of sediment were collected per fecal sample—one for morphology used in this study, and one for future molecular identification of larvae.

Identification of the L_3-stage larvae was performed to gain preliminary data on the diversity of strongyle genera present in the elephants. Larvae were identified to genus according to morphometric criteria described by Condy (1973), which include total length of larvae as measured from the extreme tail of the larva to the distal tip of the sheath, as well as length of tail and length of tail sheath. In combination, these three criteria provided a systematic and consistent basis for classification of the larvae occurring in the samples. The larval stages of other strongyle species known to occur in elephants have not been described (Condy, 1973), so our study was limited to the extent of the data currently available.

Data analysis

Because the skew index (the amount by which the values are distributed around the mean) for the EPG variable was 4.51, and above the acceptable criterion of 3.00 (Kline,

TABLE 2. Average number of strongyle eggs per gram (EPG) in feces and standard deviation (SD) for bull African elephants (*Loxodonta africana*) observed more than once in 2007, 2008, and 2009 in Etosha National Park, Namibia.

Bull ID	Times observed	Year(s) observed	Average EPG	SD
1	2	2008	2,175.00	318.20
6	5	2007, 2008, 2009	963.33	545.49
19	9	2008, 2009	1,638.89	820.36
22	8	2007, 2008, 2009	1,197.50	638.23
25	4	2007, 2008	987.50	696.87
30	2	2008, 2009	1,750.00	212.13
37	5	2007, 2008, 2009	1,105.00	647.21
38	4	2007, 2009	1,812.50	442.77
39	8	2007, 2009	1,793.75	1,398.84
40	5	2007, 2009	1,020.00	400.94
46	10	2007, 2008, 2009	1,595.00	730.47
48	3	2007, 2008	483.33	450.92
61	9	2007, 2008, 2009	1,511.11	484.03
65	3	2007, 2008, 2009	783.33	404.15
70	2	2008, 2009	2,237.50	1,255.11
77	6	2007, 2009	2,150.00	628.49
78	8	2007, 2008, 2009	1,506.25	827.40
83	2	2009	1,300.00	707.11
88	7	2007, 2008, 2009	1,232.14	1,261.01
89	3	2009	1,016.67	850.49
92	2	2009	2,125.00	459.62
96	3	2008, 2009	1,316.67	960.90
98	2	2009	500.00	636.40
100	7	2009	1,265.00	547.33
101	4	2009	1,206.25	700.11
103	2	2009	1,975.00	247.49
105	6	2007, 2009	1,525.00	1,365.19
111	2	2009	1,850.00	848.53
113	2	2008	550.00	0.00
125	2	2008	600.00	636.40
145	2	2009	1,050.00	212.13
146	2	2009	1,100.00	777.82

2005), the EPG variable was transformed using a square-root function. The skew index of the transformed EPG variable was 0.35. The transformed EPG variable was used in subsequent statistical analyses.

We compared the mean EPG 1) among age classes of bulls and family group members, 2) between bulls in musth vs. nonmusth, and 3) in bulls in the dry year of 2007 vs. the wet years of 2008 and 2009. Statistical analysis of the relationship between group type and age on strongyle EPG was done using an analysis of variance in JMP IN version 4. The square-root-transformed egg counts were used as the dependent variable and the categorical variables sex, age, and the interaction term sex*age as independent variables. Age was treated as an ordinal categorical variable. Independent sample *t*-tests assuming equal variance were calculated to compare the EPG between three-quarter- and full-size musth and nonmusth bulls, and between the wet and dry years using Microsoft Excel. A *P*-value of <0.05 represented statistical significance. All means are presented with the 95% confidence interval.

RESULTS

Family group members had significantly more EPG than bulls (family group mean = 975.71 ± 134.55; bull mean = 735.79 ± 84.40, $F=4.258$, df = 1, $P=0.041$). Although age alone was not significantly related to EPG, there was a significant interaction between age and group composition (age: $F=0.402$,

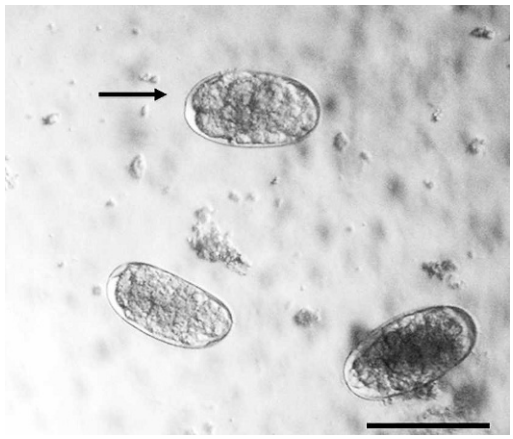

FIGURE 2. Strongyle nematode eggs from African elephants (*Loxodonta africana*) from Etosha National Park, Namibia. Typical strongyle eggs are 70–90 μm, oblong, morulated, and have a thin, translucent shell (Bowman et al., 2003). 40× (bar=approximately 100 μm).

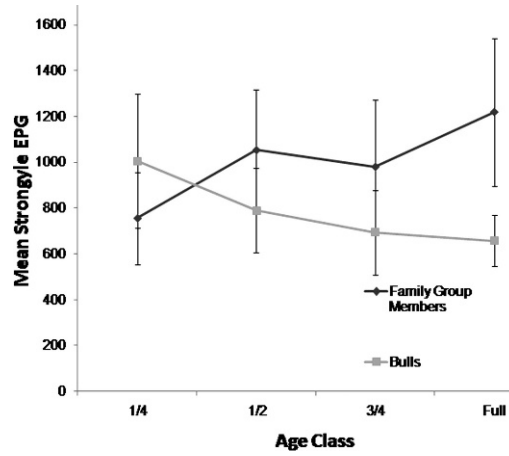

FIGURE 3. Mean strongyle eggs per gram (EPG) of feces as a function of age and group composition for African elephants (*Loxodonta africana*) in Etosha National Park, Namibia. Within the family group members, EPG increased with age; for bulls, EPG decreased with age ($P=0.004$). Full-size family group members had significantly more EPG than one-quarter-size family group members ($P=0.013$); full-size bulls had significantly fewer EPG than one-quarter-size bulls ($P=0.021$). See text for explanation of size categories.

df=3, $P=0.752$; group composition*age: $F=3.969$, df=3, $P=0.009$; Fig. 3). In bulls, strongyle EPG were significantly higher in younger animals than in older animals, whereas in family group members, the EPG were significantly lower in the younger animals than in older animals (interaction between group composition and age comparing one-quarter-size to full-size animals: $\beta=-3.9\pm1.3$, $t=-2.90$, $P=0.004$; Fig. 3). No other interactions among age classes and group composition were statistically significant.

There were significantly higher EPG found in bulls during the dry year (mean=1352.47±214.70, $n=28$) than the wet years (mean=751.39±79.02, $n=91$, $t=5.92$, df=116, $P=0.001$). To visualize this pattern we present the EPG obtained from seven individual bulls sampled in all 3 yr (Fig. 4). We found that EPG did not differ between three-quarter- and full-size musth (mean=590.28±200.47, $n=8$) vs. three-quarter- and full-size nonmusth bulls (mean=695.02±105.62, $n=52$; $t=-0.96$, df= 0, $P=0.103$).

Infective stage-L_3 larvae from three genera were identified in representative fecal samples obtained from each group. The larvae observed included *Murshidia* spp., *Quilonia* spp., and *Khalilia* spp., which were classified according to the primary criteria of Condy (1973). Preliminary screening of larvae demonstrated *Quilonia* (~800 μm) to be the most common, followed by *Khalilia* (>900 μm), and *Murshidia* (<700 μm) as the least frequently observed (Fig. 5).

DISCUSSION

The relationship between age and strongyle EPG in African elephants differed significantly with group composition. Among the family group members, as age increased, EPG increased; but among the bulls, as age increased, EPG decreased. This variation may be due to the differences in group sizes between sexes. Elephants live in fluid fission–fusion groups: typical elephant family groups are made up of an older, mature female (the matriarch) and her close relatives, including the matriarch's offspring, her

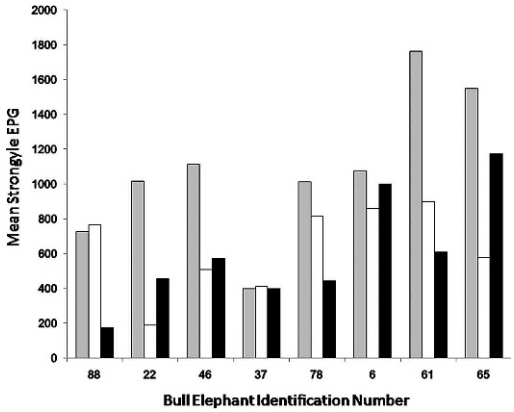

FIGURE 4. Mean strongyle eggs per gram (EPG) in seven bull African elephants (*Loxodonta africana*) in Etosha National Park, Namibia, in a dry year (2007; gray bars) and wet years (2008 [white bars] and 2009 [black bars]). Note pattern of higher EPG in dry year than wet years.

sisters, and their offspring (Buss, 1961). Family group members live and travel in tightly knit groups comprising six to 40 elephants (Buss, 1961).

Bulls, in contrast, leave their matriarchal family groups at sexual maturity (~13–15 yr of age) and tend to live in loose association with other bulls (Poole, 1989a). In addition, bulls and family groups are likely to have differences in their exposure to gastrointestinal strongyle parasites, including but not limited to territory sizes (bulls are known to cover much larger areas than matriarchal family groups [Laws, 1970; Shannon et al., 2006]), spatial and temporal contact (family group members are in close contact with all family group members continually, in contrast to looser associations between bulls), and exposure to forage contaminated by feces (because family groups tend to be made up of many more individuals, their ability to contaminate the environment with parasites is much greater).

The rate at which the environment is contaminated by parasite eggs is directly correlated with the number of infected animals in the population (Arneberg et al., 1998; Bowman et al., 2003). Our finding that the average number of parasite EPG

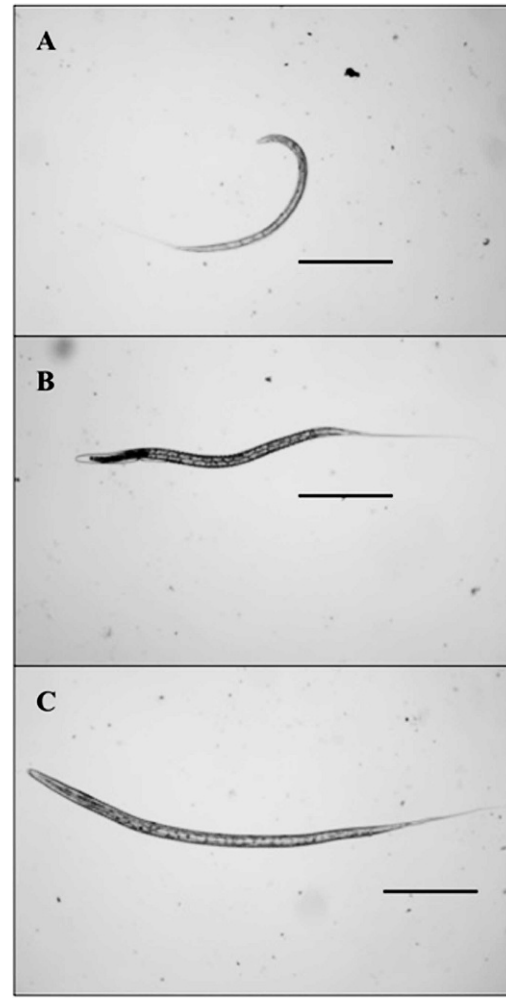

FIGURE 5. Nematode larvae identified in representative cultured fecal samples from African elephants (*Loxodonta africana*) in Etosha National Park, Namibia. A. *Murshidia*, <700 μm; B. *Quilonia*, approximately 800 μm; and C. *Khalilia*, approximately 1,000 μm. 4× (bars=200 μm).

was significantly higher in family group members than in bulls also indicates that increased host population density increases parasitic infection.

This finding is in contrast to the general trend of nematode infection in birds and mammals, that males tend to have higher parasite loads than females (Poulin, 1996). There are two potential elephant-specific explanations for our findings: 1) bulls tend to associate with fewer individuals than

family group members, which may decrease their exposure to strongyles; and 2) older, more dominant males may have access to the highest-quality resources (Poole, 1989a), thereby decreasing their exposure.

The oldest family group members had significantly greater EPG than the youngest members. Although it is hypothesized that the oldest (and most dominant) females in the herd have access to the best resources and therefore should be exposed to fewer parasites, it is possible that because older elephants eat more than young elephants, they may be exposed to a greater number of parasites. Similarly, it may be possible that elements of the mother's milk are protective for nursing elephant calves (Mota-Ferreira et al., 2009). Additionally, older elephants would have been exposed to the dense herd environment for a longer time than the youngest elephants, and could have accumulated parasites over time.

A recent transition from a densely populated family to a smaller bull group suggests that the high parasite loads that we found in the smallest bulls were established before leaving the family group. In contrast, older bulls that have been isolated from their matriarchal family group of origin for a much longer period have been living in a less dense population and therefore may have decreased exposure to parasites, explaining the lower number of EPG found in older bulls.

Additionally, because older bulls tend to be more dominant (Poole, 1989b), they likely have access to the highest quality of food, cleaner water, and an advantage over the other bulls in obtaining resources. They also may have developed resistance to parasites with age, as seen in cattle (Bowman et al., 2003). If this were the case, perhaps recurring exposure for adult females overrides any potential resistance, which could explain why this might only be true for bulls.

We found that the average strongyle EPG was higher in bulls in the dry year than in the wet years. Similarly, Vidya and Sukumar (2002) showed that parasite loads were significantly higher during the dry season than the wet season for Asian elephants in southern India. However, studies have shown that risk of parasite infection increases with grazing close to the ground compared with browsing shrubs and trees (Apio et al., 2006). This would suggest that elephants might have increased parasites during wetter years when there is a greater availability of grass.

Our finding of more parasites in the dry year may indicate that elephants are more susceptible to parasites because of nutritional stress, which may impair immunity (Coop and Holmes, 1996), or that they are potentially in contact with more parasite larvae, concentrated around decreased resources (Arneburg et al., 1998). In the dry season, access to water resources is limited, causing the density of individuals at available water sources to increase, potentially increasing the exposure of individuals to parasites (Krecek et al., 1989; Masangane, 2004). Environmental conditions have also played a role in parasite density in other species, as is the case with small equine strongyles whose movement from soil onto grasses is timed during optimal conditions that allow maximum transmission between infected and susceptible hosts (Soulsby, 1982).

Because bulls have to be fit to enter musth (testosterone being costly to produce), parasite levels might be lower for these bulls (Ganswindt et al., 2005). In addition, bulls in musth do not tend to associate with other bulls, but instead roam independently, searching for estrus females (Poole, 1999), in which case lower contact with other bulls might also influence parasite load. Bulls in musth are typically more restless and eat and drink less than nonmusth bulls, and therefore create a negative energy balance (Ganswindt et al., 2005). It is possible that this negative energy balance might result in

decreased ability to fight infection (Poole, 1999).

Because of this possibility, we hypothesized that bulls in musth may have increased parasite loads. Our results, however, showed no significant differences in EPG between three-quarter- and full-size musth and nonmusth bulls. This may be due to the small sample size of bulls in musth ($n=8$), because musth is a rare event and bulls in musth do not defecate as often as nonmusth bulls. Because musth is transitory, a bull is unlikely to drastically change his exposure to parasites while in musth and, therefore, it is more likely that a bull in better condition—with fewer parasites—would be capable of entering musth. Finally, because bulls in musth defecate less frequently than nonmusth bulls (Ganswindt et al., 2005), but the nematodes still produce eggs at the same rate, it is possible that there is an inflated EPG in musth bulls.

We looked at the difference between only full-size musth and nonmusth bulls, because full-size bulls are able to maintain musth longer (Poole, 1989b), to see if age of the bull in musth made any difference to the analysis, but it did not. In the future, we hope to have a larger sample size of musth bulls to confirm this finding.

These results indicate that environmental factors, age, and group composition affect EPG in elephants, whereas certain physiologic influences, such as musth, may not. We observed a unique pattern of bull elephants showing decreased parasite infection with age, with family group members showing increased EPG with age. We found that bulls have significantly fewer EPG than family group members, counter to most findings in the literature, which may be due to elephant group dynamics.

This sampling of EPG in elephants in Etosha National Park provides a general understanding of strongyle infections in this wild population, and better insight into the interplay of environment and elephant biology, which may be applied to managing wild elephant populations. Further studies are underway to more extensively determine the prevalence of each strongyle genus within specific subcategories of elephants, and to conduct molecular genetic analyses to determine the species within each genus we have identified.

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