

RESEARCH ARTICLE

Fitness Impacts of Tapeworm Parasitism on Wild Gelada Monkeys at Guassa, Ethiopia

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Parasitism is expected to impact host morbidity or mortality, although the fitness costs of parasitism have rarely been quantified for wildlife hosts. Tapeworms in the genus *Taenia* exploit a variety of vertebrates, including livestock, humans, and geladas (*Theropithecus gelada*), monkeys endemic to the alpine grasslands of Ethiopia. Despite *Taenia*'s adverse societal and economic impacts, we know little about the prevalence of disease associated with *Taenia* infection in wildlife or the impacts of this disease on host health, mortality and reproduction. We monitored geladas at Guassa, Ethiopia over a continuous 6½ year period for external evidence (cysts or coenuri) of *Taenia*-associated disease (coenurosis) and evaluated the impact of coenurosis on host survival and reproduction. We also identified (through genetic and histological analyses) the tapeworms causing coenurosis in wild geladas at Guassa as *Taenia serialis*. Nearly 1/3 of adult geladas at Guassa possessed ≥1 coenurus at some point in the study. Coenurosis adversely impacted gelada survival and reproduction at Guassa and this impact spanned two generations: adults with coenuri suffered higher mortality than members of their sex without coenuri and offspring of females with coenuri also suffered higher mortality. Coenurosis also negatively affected adult reproduction, lengthening interbirth intervals and reducing the likelihood that males successfully assumed reproductive control over units of females. Our study provides the first empirical evidence that coenurosis increases mortality and reduces fertility in wild nonhuman primate hosts. Our research highlights the value of longitudinal monitoring of individually recognized animals in natural populations for advancing knowledge of parasite-host evolutionary dynamics and offering clues to the etiology and control of infectious disease. *Am. J. Primatol.* 9999:1–16, 2015. © 2015 Wiley Periodicals, Inc.

Key words: wildlife disease ecology; parasites; reproduction; mortality; *Taenia serialis*

INTRODUCTION

The relationship between a parasite and its host is not unlike that between a predator and its prey—like predators, parasites are intimately connected to their host (prey) in a trophic interaction that has important consequences for both interactants [Hudson et al., 2002]. While parasites benefit from

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Received 25 March 2014; revised 17 December 2014; revision accepted 22 December 2014

DOI: 10.1002/ajp.22379
Published online XX Month Year in Wiley Online Library (wileyonlinelibrary.com).

exploiting their hosts, parasitism is expected to result in reduced host fitness because energy that parasites usurp from their hosts is energy that hosts could have directed towards their own survival, growth and reproduction [Moller, 1997]. Evidence consistent with this hypothesis has been mounting in recent decades [e.g., [Devevey & Christe, 2009](#); [Knowles et al., 2010](#); [Tompkins & Begon, 1999](#)], as has the recognition that parasites can exert significant influences on host species population dynamics [e.g., [Hudson et al., 1998](#)] and evolution [e.g., [Garamszegi & Nunn, 2011](#)]. Despite numerous advances in our understanding of wildlife disease ecology [Hudson et al., 2002; [Tompkins et al., 2011](#)], our knowledge of the effects of parasites on natural populations—including how, when, and by how much they reduce host fitness—remains woefully incomplete [[Pioz et al., 2008](#)]. In this study, we provide the first evidence of reductions in survival and fertility associated with tapeworm infection in wild nonhuman primates, and evaluate the ecological and evolutionary implications of these findings for both the parasites and their primate hosts.

Research into the impacts of parasitism on host fitness in natural wildlife populations often utilizes parasite load manipulation experiments. By disrupting host-parasite systems away from their equilibrium levels, these experiments enable researchers to study the consequences of these disruptions for the host [[Tompkins & Begon, 1999](#)]. Some studies have found that experimental reductions in parasite load increased the fertility of treated hosts, while others have found that reduced parasite loads enhanced host survival [reviewed in [Tompkins & Begon, 1999](#); [Tompkins et al., 2002](#)]. To date, however, most prior studies have focused on only a handful of species, primarily short-lived birds and a few mammals [[Tompkins et al., 2002](#)]. Research is needed on a greater diversity of wildlife host-parasite systems for a more complete understanding of the “general” contributions of parasites to host fitness to emerge [[Thompson et al., 2010](#); [Tompkins & Begon, 1999](#)]. However, it is not always logistically feasible or ethically desirable to carry out experimental perturbations of parasite load in wildlife hosts. In such cases, researchers must rely on data from longitudinal monitoring and other less invasive evidence of host-parasite interactions to infer the influence that parasites have on their wildlife hosts [[Thompson et al., 2010](#)]. Among host-parasite systems, terrestrial nonhuman primates and their parasitic worms have been understudied despite their potential to serve as model systems for human-helminth interactions and their ecological importance in terrestrial ecosystems [[Huffman & Chapman, 2009](#)].

Parasites can be roughly divided into two general groupings: micro- and macroparasites. Compared to microparasites, macroparasites (which include par-

asitic worms, or helminths, and arthropods) are larger, have longer generation times and often cause chronic infections and disease [[Hudson et al., 2002](#)]. Tapeworms, or cestodes, are considered to be among the most successful of the helminths [[Despommier, 2013](#)]. Tapeworms are speciose and exploit a remarkable diversity of vertebrate and invertebrate hosts across the globe [[Despommier, 2013](#)]. One explanation for their success may be their complex life cycle [[Despommier, 2013](#)]. Tapeworms typically exploit at least two different hosts and require at least two transmission events to complete one life cycle. In the first of the two transmission events, an infected definitive host (usually a carnivore) sheds eggs (produced by adult tapeworms living in its digestive tract) in their feces into the environment. Intermediate (usually herbivorous) hosts become infected by eating vegetation covered with the eggs, which then develop into the worm’s larval stage inside its new host. The second transmission event occurs when an infected intermediate host is consumed by a definitive host. Once this happens, the larvae develop into reproductively mature adults (in the definitive host) capable of producing eggs which would then leave their definitive host, to start another life cycle [[Hoberg, 2002](#)].

For cestodes, tapeworms in the genus *Taenia* are unusual in that they almost always use mammals as both intermediate and definitive hosts, including livestock and humans [[Hoberg, 2002](#)]. Humans can become infected with tapeworms in a variety of ways, including drinking water (or eating foods) contaminated with tapeworm eggs, eating undercooked intermediate hosts and using infected flesh as a poultice [[Despommier, 2013](#)]. The symptoms and diseases associated with tapeworm infection vary widely among and within host populations. In humans (and other animals), infection (of the intermediate host) with the worm’s larval stage causes *coenurosis*, while infection (of the definitive host) with the adult stage causes *taeniasis*. Taeniasis is the most common form of *Taenia* infection in humans and is considered among the world’s leading neglected tropical diseases [WHO, 2013]. Indeed, taeniasis in humans and livestock causes global annual financial losses in excess of USD 3–4 billion [[Hoberg, 2002](#)] and untold morbidity and mortality in humans. In addition to their health effects, *Taenia* (and other related worm) infections can hinder socioeconomic development of infected communities by impairing physical and mental growth in children, thereby hindering their educational achievement [[Hotez et al., 2006](#)]. Most of these costs are borne primarily by people in underdeveloped countries [[Hoberg, 2002](#)].

Despite their ubiquity and societal and economic importance, our incomplete knowledge of the diversity and life cycle of tapeworms (and other macroparasites) has “hindered our full understanding of

their host associations—final and intermediate—and their potential for causing disease” [E. P. Hoberg in Becker, 2001; pg. 16]. Moreover, measures to effectively control parasitism in vulnerable species or populations must not only rely on epidemiological data from infected populations, but also on a more complete understanding of the evolutionary ecology of the pathogenic agent(s) involved, including their life cycle and impacts on wildlife hosts [Poulin, 2007]. Unfortunately, data essential to advance our understanding of these topics, especially the impacts of parasites on wildlife hosts, are scarce for two reasons: the challenges associated with (a) longitudinal monitoring of individually-recognized animals and (b) determining the nature (and magnitude) of the fitness costs of parasitism in natural settings [Hudson et al., 2002; Scott, 1988]. These data are vital to our understanding of current and emerging threats to human health and biodiversity, especially for vulnerable species or populations [Daszak et al., 2000; Scott, 1988].

Nonhuman primates, namely geladas (*Theropithecus gelada*), terrestrial monkeys endemic to the alpine grasslands of Ethiopia, also suffer from disease associated with tapeworm infection, particularly coenurosis. In geladas, larvae of the tapeworm *Taenia serialis* have been reported to form large subcutaneous fluctuant cysts (coenuri) in both captive [Clark, 1969; Kaufmann & Whittaker, 1972] and natural populations [Dunbar, 1980; Ohsawa, 1979; Schneider-Crease et al., 2013]. Estimates of the prevalence rate of coenurosis in wild geladas at two different time points separated by three decades in the Simien Mountains National Park, a site with a long history of intensive disturbance by humans and their livestock, range from 5% [Schneider-Crease et al., 2013] to 11% [Dunbar, 1980]. Virtually nothing is known, however, about the prevalence and impact of coenurosis in geladas inhabiting ecologically intact environments less dominated by humans and livestock where geladas are the dominant herbivores and likely exert large impacts on vegetation dynamics and ecosystem processes.

The wild gelada population at Guassa, Ethiopia is an ideal one in which to non-invasively investigate macroparasite contributions to the fertility and survival of a wildlife host for several reasons. First, signs of the disease associated with infection by tapeworm larvae, coenurosis, are readily observable. Second, Guassa’s Afroalpine ecosystem contains an intact carnivore community and is, to our knowledge, the largest remaining habitat of its kind and one that likely resembles the environments in which geladas evolved [Fashing et al., 2014]. Finally, the population has been under continuous monitoring since January 2007, so much is known about the demographic, reproductive and social status of the animals in the study population.

In the present study, using molecular and histological techniques, we identify the *Taenia* sp. causing coenurosis in the wild gelada study population at Guassa, Ethiopia. Because the parasites appear to hijack and reroute host animals’ energy budgets towards their own survival and reproduction, forming large protuberant cysts in geladas, we also sought to evaluate the extent to which they impact gelada fitness (survival and reproduction) at Guassa using longitudinal data from our ongoing 6½ year field study at this site. We predicted that coenurosis resulting from *Taenia* parasitism in geladas would negatively impact host animal survival. We also predicted that coenurosis would adversely affect fertility among adult males and females. We discuss our findings in light of recent advances in understanding of parasite-host evolutionary dynamics, focusing in particular on the consequences of tapeworm parasitism for individual hosts and populations. We also explore how our findings contribute to ongoing discussions about why some diseases (and their associated pathogenic agents) are more virulent (i.e., cause more harm) than others.

METHODS

Subjects and Study Population

Geladas (a distant relative of baboons, *Papio* spp.) are sexually dimorphic, terrestrial cercopitheicine monkeys endemic to the alpine grasslands of the Ethiopian Highlands. Geladas are unusual among primates in that they feed primarily on grasses and sedges, spend the night on cliffs, and live in multi-tiered societies [Dunbar & Dunbar, 1975; Fashing et al., 2014; Iwamoto, 1993; Mori et al., 2003]. The fundamental level within gelada society is the polygynous *one-male unit* (OMU), usually consisting of a single male, an average of four adult females (henceforth referred to as the *harem* of females under a male’s reproductive control), and their dependent offspring, though sometimes additional adult males (follower males) are present in the unit as well [Kawai et al., 1983]. OMUs that share a common home range are referred to as *bands*, though OMUs belonging to the same band do not necessarily range together every day. Those OMUs observed ranging together on any given day in temporary aggregations are called *herds* [Kawai et al., 1983].

We conducted our study of wild geladas on the Guassa Plateau, a large (111 km²) and unusually ecologically intact Afroalpine tall-grass ecosystem located along the western edge of the Great Rift Valley (10°15’–10°27’N; 39°45’–39°49’E) at elevations between 3,200 and 3,600 m asl [for further details, see Ashenafi, 2001; Fashing et al., 2014]. Protected by an indigenous conservation system dating to the 17th century [Ashenafi & Leader-Williams, 2005], Guassa is probably the largest tall-

grass ecosystem remaining in the Ethiopian Highlands and retains an intact large carnivore community, including Ethiopian wolves (*Canis simensis*), cryptic African wolves (*Canis aureus lupaster*), spotted hyenas (*Crocuta crocuta*), servals (*Leptailurus serval*), and leopards (*Panthera pardus*) [Ashenafi, 2001; Ashenafi & Leader-Williams, 2005; Rueness et al., 2011]. Guassa is dominated by the perennial tall grass *Festuca macrophylla* (Poaceae), though many other perennial grass or sedge species and a variety of forb and shrub species are present as well [Fashing et al., 2014].

Our study focused on a ~220-member gelada band (Steelers Band) at Guassa. We began habituating the members of this band to the presence of observers in December 2005. By January 2007, when we began systematic data collection (on a near-daily basis), we could recognize most individuals in the band based on natural markings including scars, facial crease patterns, head shape, external parasitic cysts and other distinctive features.

Data Collection

Data for this study were collected by Nguyen, Fashing and fourteen Guassa Gelada Research Project (GGRP) team members working in pairs (JTK & VVV; LML & NON; TSB & CBG; RJB & SZJ; KMS & TJT; BSK & CMM; MSR & JDR) from January 2007 through June 2013. GGRP team members were university graduates with prior research experience who underwent additional training (≥ 6 weeks) before contributing to the data collection. Throughout the study period, repeated checks were carried out in the field to ensure that inter-observer reliability remained high. During the 6½ year study period (Jan 2007–Jun 2013), we monitored the demographic, reproductive, and health status of all members of 16 OMUs belonging to a single band (though one OMU dissolved in 2009 after the non-simultaneous deaths of both of its adult females), including 99 adult females and 68 adult males, on a near-daily basis. OMUs at Guassa contained 1–9 adult females and 1–3 adult males. Units with multiple males were uncommon, and except on a few occasions, one male (i.e., the leader male) performed all of the matings visible to researchers in these units. All study individuals were habituated to the presence of observers on foot at distances of 1–5 m. Our research adhered to the American Society of Primatologists principles for the ethical treatment of primates.

Demographic Data

On each study day, we recorded all demographic changes (i.e., births, deaths, emigrations, immigrations) occurring in the study units. Because of our near-daily monitoring of the study units, nearly all

births that were not directly witnessed were recorded within 1–6 days after birth. Deaths that were not directly witnessed could, in many instances, be inferred from prolonged absences (following extensive searching) from the near-daily censuses. For adult females, disappearances from the study band were presumed to result from death rather than dispersal since female geladas typically remain in their unit of birth throughout their life [Bergman & Beehner, 2013] and were not known to disperse from one unit to another at Guassa. Indeed, missing females were never seen again in another unit or band. For adult males, disappearances from the study band can result from changes in reproductive status (e.g., following a male replacement event, where one male successfully assumes control over a harem of females from another male) and may reflect dispersal from one social unit to another. Based on our collective experience directly observing the deaths of several males, we considered adult males who met one or both of these conditions to have died: (1) suffered a male replacement event that resulted in severe bodily trauma or injury to themselves (and in some cases the death or disappearance of infants sired during their tenure) or (2) were visibly declining in bodily health and vigor in the days or weeks prior to their disappearance. All other males who were otherwise healthy but never seen again after they disappeared from the study units were presumed to have dispersed to other, non-study bands in the population. To date, we have data sufficient to confidently assign a demographic status (alive or dead) to 94 of the 99 adult females and 40 of the 68 adult males in the study population. We do not know the current demographic status for five adult females (all members of a single unit that moved out of the main study area) and 28 adult males who could have dispersed to other parts of the study area.

Cause of death was not always known but could sometimes be inferred from records of an animal's physical condition in the days prior to their disappearance and may include predation, illness or injury (both of which may make animals susceptible to predation). In several cases, the remains of geladas—sometimes partially consumed, sometimes intact—were found shortly after an individual was reported to have disappeared and presumably died.

Adults were classified as either “prime” or “old” at the time of death based on records of their physical condition when they were last seen alive. Adults were designated as “prime age” at death if they appeared to be in early to middle adulthood, showing no signs of the aging obvious in “old” individuals (e.g., wrinkled face, sagging buttocks, and shaggy, rough coat). For females, “old” individuals also tended to exhibit a patchier distribution of pinks and blacks in their paracollosoal skin and more unevenly patterned chest beads during reproductive cycles than young or middle age females.

Reproductive Data

On each study day, we recorded all changes in the reproductive status of all adult members of the study units. For females, we assessed the reproductive status of each individual by monitoring changes in the size and color of any swellings on the chest or perineum following McCann [1995]. Pregnant females could be identified several months before birth based on a gradual pinkening of the skin on their perineum [McCann, 1995]. At Guassa, female geladas produce their first offspring at ~6 yrs of age and produce one additional offspring every 2–3 yrs thereafter, values roughly consistent with those reported for geladas elsewhere [Dunbar, 1979; Kawai, 1979; le Roux et al., 2011]. We also monitored all changes in male reproductive status. During the study period, all instances of takeovers—the replacement of the reproductive (oftentimes sole) male in the social unit by an immigrant adult male—were recorded for each of the 16 one-male study units.

Health Data

We regularly monitored changes in the health of all individually-known geladas in the study population, including all wounds, injuries and symptoms of disease or other pathologies. Symptoms of disease and other pathologies include cystic structures (apart from sexual skin swellings on the chests and perineums of females), unusual redness or swelling around the eyes, diarrhea, vomiting, stiffness of the limbs or fingers, limping, indications of fatigue or weakness, tremors or convulsions, persistent coughing and sneezing, unexpected discharges from any part of the body (including the presence of worms in the feces), and excessive thinning or lightening of the coat. For cystic structures, we recorded their approximate size and location on the body and whether afflicted animals had problems with movement or with other bodily functions. We continued to monitor all cystic structures (from the date they were first observed) for as long as animals possessed them (i.e., several months to years) to track changes in their morphology (e.g., shape, color, condition).

Parasite Material Collection & Species Identification

During 3 days in June 2013, we followed an adult female gelada (Frodo) with a large fluid filled parasitic cyst in her lumbar region. At this time, Frodo's cyst had ruptured and begun leaking parasitic material onto the surrounding environment (Fig. 1A). On occasion, Frodo, like other geladas with ruptured cysts, would ingest the parasitic material that fell from her leaking cyst onto her fur. To identify the parasite present in the cyst, we non-invasively obtained several samples of the material

from Frodo's ruptured coenurus (including both liquid and solid components) that had fallen onto nearby rocks or vegetation after she left the area, depositing the materials into 2 ml low-binding DNA Eppendorf tubes prefilled with RNALater (Applied Biosystems/Ambion, Austin, TX, USA). We obtained a sufficient amount of parasitic material to perform both histological examinations and molecular biological analyses at the German Primate Center (DPZ) in Göttingen, Germany.

To carry out the histologic exam, a representative part of the RNALater solution preserved material was embedded into paraffin using an automated system (Thermo Shandon Hyper Center XP Tissue Processor, ThermoFisher Scientific, Waltham, MA, USA). The paraffin block was then cut into a series of 4 µm thick tissue layers, which were transferred onto slides. Specimens were allowed to dry over night at 37 °C. Hematoxyline-Eosine (H&E, Merck, Darmstadt, Germany) and Periodic-Acid-Shiff (PAS, Merck, Darmstadt, Germany) staining was performed using a fully automated process (Varitain Gemini, Thermo Shandon).

Total genomic DNA from the collected material was extracted using the First-DNA-All-Tissue-Kit (Gen-ial, Troisdorf, Germany) following the manufacturer's instructions. To identify the *Taenia* sp. present in our sample, we PCR-amplified and sequenced fragments of the mitochondrial cytochrome *c* oxidase subunit 1 (*cox1*) and 12S rDNA genes [von Nickisch-Roscnegk et al., 1999] following Bowles et al. [1992]; Gasser et al. [1999] and Padgett et al. [2005], respectively. Amplification performance was checked on 1% agarose gels. The PCR products were then excised from the gel, purified with the Qiagen Gel Extraction kit (Qiagen, Hilden, Germany) and sequenced on an ABI 3130xl sequencer using the BigDye Terminator Cycle Sequencing kit (Applied Biosystems, Life Technologies GmbH, Carlsbad, CA, USA) and the respective amplification primers. Subsequently, sequences were analyzed, edited, and aligned against available orthologous sequences from congeners using 4Peaks (version 1.7.2, Mek&Tosj.com) and SeaView version 4 [Gouy et al., 2010]. To identify the *Taenia* sp. present in our sample, we performed a standard nucleotide BLAST search at the NCBI homepage. Moreover, we directly compared our 12S rDNA sequence with the one recently published from *T. serialis* derived from a gelada from the Simien Mountains National Park, Ethiopia [Schneider-Crease et al., 2013]. The sequences obtained from our sample are deposited at GenBank (GenBank IDs: KJ490640, KJ859226).

Data Analysis

From Jan 2007 to June 2013, we monitored a total of 348 geladas at Guassa for obvious signs of the disease associated with tapeworm infection. Following Scott [1988], we define infection as the presence of a

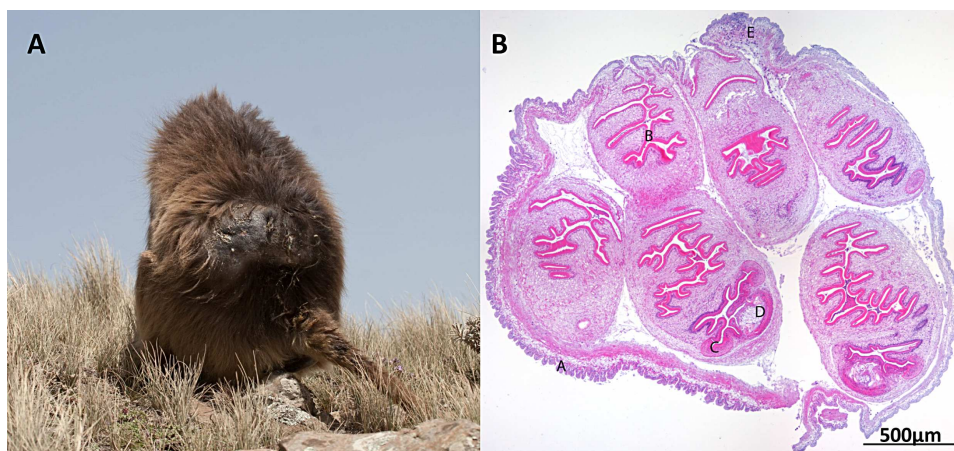


Fig. 1. (A) Adult female gelada (Frodo) at Guassa, Ethiopia with a focally ruptured *Taenia serialis* coenurus located on the lower left back above the tail. Parasitic material from Frodo's coenurus which fell to the ground was non-invasively collected for later histological and genetic analyses. (B) Microscopic view of a brood capsule from Frodo's *T. serialis* coenurus. A: Pseudostratified cuboidal to columnar epithelial-like structure on the exterior of the brood capsule; B: Inner tegument with eosinophilic cuticle; C: Section of a sucker; D: Tube-like hooks that indicate the rostellum; E: Focal infiltration of eosinophile granulocytes and histiocytes. H&E staining.

parasite within a host and disease as “a clinical condition that can be observed or measured” (pg. 41). Since we cannot confirm infection status visually or rule out the possibility that infected individuals may not exhibit externally visible signs of infection, we consider geladas with one or more cystic structures as exhibiting symptoms of the disease associated with tapeworm infection. The prevalence rates we report below are of obvious signs of disease, not infection. Since tapeworms, like other macroparasites, often cause chronic infection and disease, the disease prevalence rates we report below span the entire 6 ½ year study period, instead of a single point in time. Individuals without parasitic cysts are considered to be “disease free”, and may be free of infection or only recently infected (i.e., at an early stage of developing a coenurus). Of course, we cannot rule out the possibility that some of these individuals may possess (smaller) internal parasitic cysts not visible to observers.

The vast majority of geladas with cysts at Guassa were adults. We evaluated the influence of the disease associated with tapeworm infection on adult survival by comparing mortality for adults of each sex who possessed parasitic cysts to members of their sex without cysts over the 6½ year study period using the G-test for independence for females ($n = 94$) and Fisher's exact test for males ($n = 40$) because the small sample size prevented us from using the G-test for males as well.

To ascertain whether the increased mortality rate among adults with coenuri resulted from them being substantially older than adults without coenuri, for adult members of each sex that died during the study period, we compared the proportion of individuals with and without cysts that were in their “prime” at death. For this analysis, we used the G-test

for independence for females and Fisher's exact test for males because the small sample size prevented us from using the G-test for males as well.

To evaluate the impact of maternal cysts on offspring survival, we compared survivorship for offspring whose mothers possessed parasitic cysts at the time of the offspring's birth with offspring whose mothers did not possess cysts using Kaplan-Meier failure time (i.e., survival) analyses.

We further evaluated the influence of the disease associated with tapeworm infection on female fertility or reproductive rate by employing general linear model (GLM) procedures to assess the influence of the previous offspring and cysts on interbirth interval (IBI) at Guassa. Survival (or survival time) of the infant born at the start of the IBI was one of the most important (if not the single biggest) predictors of IBIs in several long-term studies of nonhuman primates [e.g., Emery Thompson et al., 2007; Fedigan et al., 2008]. In light of these previous studies, we examined the effects of (a) the survival (or death) of the previous offspring at the time of the conception of the subsequent offspring and (b) the presence (or absence) of parasitic cysts on the mother during the IBI on the length (in number of days) of the IBI. We chose GLM rather than generalized linear mixed model (GLMM) analyses because (1) despite their growing popularity, concerns have recently been raised about the widespread misuse of GLMM analyses in ecology and evolution [Bolker et al., 2009] and (2) although GLMMs provide greater flexibility for analyzing non-normal data where random effects are “a variable of interest” [Bolker et al., 2009, pg. 134], our data were normally distributed and exploring random effects was not an objective of our study.

For the IBI analysis, we treat each IBI as an independent data point (as other researchers have done [e.g., Robbins et al., 2007]), rather than pooling values for each mother since (a) we have no reason to believe that one birth will influence another and (b) we suspect that the social and ecological variables surrounding each birth (including maternal age/experience, food availability, timing since male replacement events, etc.) will have bigger impacts on IBIs than will the identity of the mother, though we do not have the power to detect such patterns in the present analyses. Our analysis consisted of 72 IBIs from 47 individual females. Since our data come from a large number of unique individuals, there is little possibility that our results are biased by a few individuals. Nearly 60% ($n = 28/47$) of the females in our study contributed a single IBI to the analysis, with the rest ($n = 19$) contributing an average of 2.3 IBIs to the analysis (range 2–4 IBIs/female). In addition, nearly 60% ($n = 11/19$) of the females contributing multiple IBIs to the analysis had IBIs in multiple categories (i.e., with cyst, without cyst, etc.) over the course of the study, so we could not use the average of their IBIs for this analysis.

All statistical analyses were conducted using SPSS 20.0.0 (2013, SPSS Inc.). Unless otherwise noted, our data met the assumptions of the statistical tests we used including, where appropriate, normality and homogeneity of variances. Values reported are means \pm SE unless otherwise noted. All analyses were two tailed with $P < 0.05$.

RESULTS

Histological and Molecular Parasite Identification

Histologic examination revealed that the exterior of the parasitic brood capsules consisted of pseudostratified cuboidal to columnar epithelial-like structures. Inside, the capsules contained multiple invaginated protoscolices (tapeworm larvae) which were grouped into small clusters (Fig. 1B). The larvae's inner tegument (which acts as the host-parasite interface and functions to protect the parasite from the host's digestive enzymes) exhibited an eosinophilic cuticle, probably produced as protection against the parasite by the host in response to the presence of the foreign proteins in the tegument. While the suckers of the parasite's head are not fully visible, large prominent tube-like hooks of approximately 95 μ m in length indicate the rostellum. The loose parenchymal stroma of the parasite contained numerous calcareous corpuscles along the invaginated necks and protoscolices which were characterized by clear spherical structures. Focally, the outer epithelium and parenchyma of the coenurus were massively infiltrated by host eosinophilic granulocytes and

histiocytes. The results of our histologic investigations indicate that our sample contained coenuri with several tapeworm larvae inside.

The comparison of our sequences with those of *Taenia* sp. deposited in GenBank revealed that the sequenced 372 bp of the *cox1* gene and the 316 bp long fragment of the 12S rDNA from Guassa are most similar to those of *T. serialis*. Our *cox1* sequence differs in only two positions (0.5%) from the orthologous sequence of the reference mitochondrial genome of *T. serialis* (AB731674) and in a maximum of five positions (1.3%) from other *T. serialis* sequences deposited at GenBank, while at least 22 differences were found in comparing our *cox1* sequence to orthologs of other *Taenia* sp. (*T. krabbei*: 22–24, 5.9–6.4%; *T. multiceps*: 22–25, 5.9–6.7%; *T. saginata*: 25, 6.7%). Our 12S rDNA sequence differs only in a single position (0.3%) from the orthologous sequence of the reference mitochondrial genome of *T. serialis* and the gelada sample from the Simien Mountains National Park (KF414739). When we compared our sequences to other *T. serialis* sequences, we found a maximum of two mutations (0.6%), while at least 10 mutations were found when we compared our 12S rDNA sequence to orthologs of other *Taenia* sp. (*T. madoquae*: 10, 3.2%; *T. multiceps*: 13–17, 4.1–5.4%; *T. asiatica*: 14–16, 4.4–5.1%; *T. saginata*: 17–19, 5.4–6.0%; *T. ovis*: 21, 6.6%). Our results thus clearly identify the *Taenia* in our sample as *T. serialis*.

Prevalence and Presentation of Tapeworm Cysts at Guassa

Approximately one of every six geladas in the study population at Guassa (16.4% or 57 of 348) possessed at least one *T. serialis* cystic structure (henceforth coenurus) during the 6½ year study period (Jan 2007–Jun 2013). Adults accounted for 87.7% of geladas with coenuri at Guassa (50 of 57). The prevalence rate of the disease among adults was 29.9% (50 of 167) while the prevalence rate among immatures was 3.8% (7 of 181). Adult geladas of both sexes were significantly more likely to possess coenuri than immature members of their sex (Fisher's exact tests, females: $P < 0.0001$; males: $P < 0.0001$; Fig. 2). Among adults, however, there was no sex difference in the prevalence of coenuri (G-test for independence, $G_1 = 0.22$, $P = 0.64$).

Coenuri varied widely in size (even within an individual over time) and were visible on all parts of the body except the tail. Among the 31 adult females with coenuri, more than half possessed cysts on the core of their body (54.8%) while coenuri on the arms (35.5%), head (25.8%) and legs (19.4%) were less common. In contrast, among the 19 adult males with cystic structures, a roughly similar percent exhibited coenuri on their legs (42.1%) and core (36.8%) while coenuri were less common on the more distal parts of

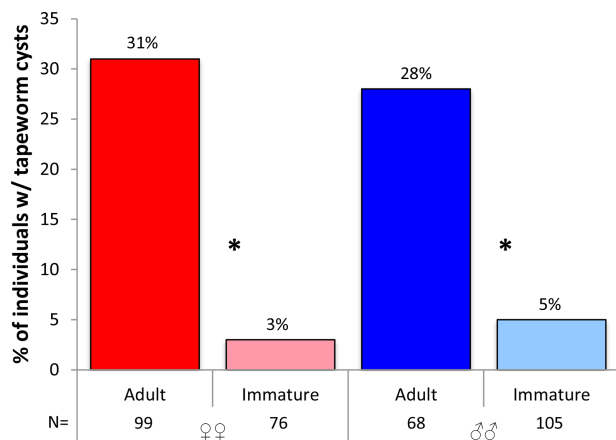


Fig. 2. The percent of adult and immature geladas of each sex with parasitic cysts at Guassa, Ethiopia over the 6½ year study period (Jan 2007–Jun 2013). Adults were significantly more likely to possess parasitic cysts than immature members of their sex (Fisher’s exact tests, females: $P < 0.000001$; males: $P < 0.0001$). * = difference is statistically significant at $P < 0.05$. Among adults, however, there was no sex difference in the occurrence of parasitic cysts (G-test for independence, $G_1 = 0.22$, $P = 0.64$).

the body (i.e., arms [26.3%] and head [15.8%]). Adult females showed a trend towards possessing coenuri in two or more regions of the body compared to adult males (41.9% of 31 females vs. 15.8% of 19 males, Fisher’s exact test, $P = 0.068$).

The prevalence of *Taenia coenuri* did not differ significantly across study units. Fifteen of the 16 focal units contained adult females with coenuri at some point during the study and the proportion of adult females with coenuri did not differ significantly across the 16 units (G-test for independence, $G_{15} = 9.55$, $P = 0.85$).

Tapeworm Cysts and Adult Mortality

Adults of both sexes with coenuri were significantly more likely to die over the 6½-year study period than members of their sex without coenuri (Fig. 3). Males with coenuri were >2.5 times more likely to die than members of their sex without coenuri (Fisher’s exact test: $df = 1$, $P = 0.01$), while females with coenuri were >2 times more likely to die than females without coenuri (G-test for independence: $G_1 = 12.49$, $P < 0.001$) (Fig. 3).

The increased mortality rate among adults with coenuri did not result from them being substantially older than those without coenuri. Indeed, most of the adults who died during the study were “prime age” at the time of their death. “Prime age” adults accounted for roughly similar proportions of the dead regardless of disease status for both sexes. “Prime age” individuals accounted for a similar percent of the dead among females that (at the time of death) possessed coenuri and those that did not

(55% of 22 vs. 65% of 21; G-test for independence, females: $G_1 = 0.23$, $P = 0.62$). Males exhibited a similar pattern—among the dead, 67% of males with coenuri ($n = 9$) and 63% of males without coenuri ($n = 8$) were in their “prime” at death (Fisher’s exact test, $P = 1.0$).

Tapeworm Cysts and Male Reproduction

Adult males with coenuri rarely successfully usurped reproductive control over a harem of females from another male. Only 2 of the 35 male replacement events (involving 33 different males) that occurred among the study units over the 6½ year study period were carried out by males who had tapeworm cysts at the time of the takeover.

Tapeworm Cysts and Female Reproduction

Impact of cysts on female fertility

The death of the previous offspring had the single biggest effect on interbirth intervals (IBIs) at Guassa. Death of the previous offspring resulted in IBIs that were ~½ of those in which the previous infant was alive when mothers conceived their subsequent offspring (858 ± 28 [$n = 51$] vs. 467 ± 38 [$n = 21$] days, $n = 72$ IBIs for 47 adult females, Table I). This variable alone explained 46.6% of the variance in IBIs at Guassa (Table I).

The presence of parasitic cysts on mothers during the IBI also explained a significant, but much smaller (6.4%), percent of the variance in IBIs in our sample (Table I). Females with coenuri required ~3–4 more months to produce subsequent offspring than females without coenuri (Fig. 4). Among females whose previous infants died before they conceived their subsequent offspring, IBIs were 134 days longer for females with cysts compared to females without them (550 ± 57 [$n = 8$] vs. 415 ± 47 [$n = 13$] days; $n = 21$ IBIs among 16 females). Likewise, among females whose previous infants were alive when they conceived their subsequent offspring, IBIs were 86 days longer for females with cysts than for females without them (921 ± 41 [$n = 14$] vs. 835 ± 34 [$n = 37$] days; $n = 51$ IBIs among 40 females).

Impact of maternal cysts on offspring survivorship

Survivorship was significantly higher for offspring whose mothers did not possess coenuri on the day of the offspring’s birth ($n = 109$ offspring to 61 females, 73 right censored individuals [i.e., those infants that are still alive as of the end of the study period, in July 2013]) than for offspring whose mothers did possess coenuri ($n = 32$ offspring to 18 females, 12 right censored individuals) (log rank test, $P = 0.006$) (Fig. 5). Because gelada offspring, like many other primate offspring, are entirely reliant on their mothers much of their first year of

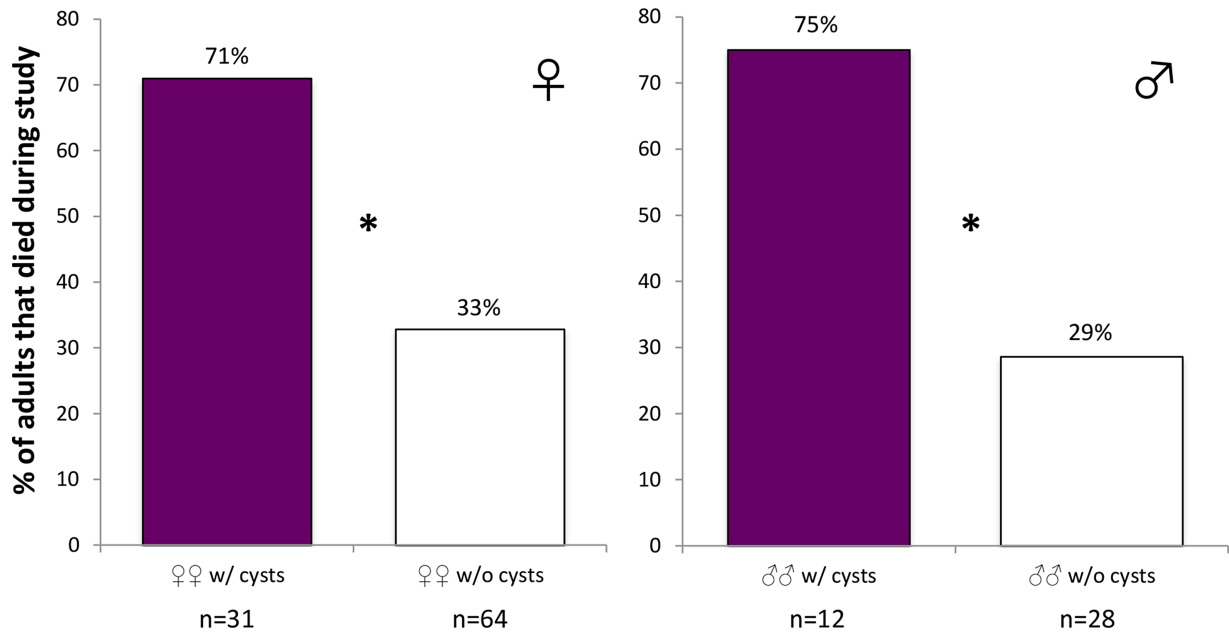


Fig. 3. The percent of adults of each sex (with and without cysts) that died during the 6½ year study period (Jan 2007–June 2013) (females (G-test for independence): $G_1 = 12.49$, $P < 0.001$; males (Fisher’s exact test): $df = 1$, $P = 0.01$). * = difference is statistically significant at $P < 0.05$. Adults of both sexes with parasitic cysts suffered significantly higher mortality than adult members of their sex without cysts.

life (Nguyen & Fashing, unpubl. data), we had to consider the possibility that this difference in offspring survivorship could have arisen from the premature death of afflicted mothers. The results of our survival analysis did not change, however, after we excluded the five infants under a year old whose mothers died the day they did (or a few days earlier) (log rank test, $P = 0.008$), suggesting that the effects of maternal parasitic cysts on infant

mortality did not arise from the premature deaths of afflicted mothers. Of the 109 infants born to mothers without coenuri, 23% died before the age of 1 year ($n = 25$ infants died before age 1, 72 did not die, 12 censored cases). In contrast, more than double this value (50%) of the 32 infants born to mothers with coenuri died before their first birthday ($n = 16$ infants died before age 1, 16 did not die, 0 censored cases).

TABLE I. Effects of Infant Mortality and Maternal Parasitic Cysts on Variation in Interbirth Intervals (IBIs) in Wild Geladas at Guassa, Ethiopia.

	Interbirth interval (IBI) in days [€]			
	Mean square	F	P	Partial Eta Squared
Overall model				
Model	815628.952	23.276	<0.0005	0.507
Error	35041.237			
Predictor Variables				
Death of previous offspring*	2078564.977	59.318	<0.0005	0.466
Maternal cyst**	161665.177	4.614	0.035	0.064

Results of the GLM indicate that the survival (or death) of the previous offspring explained a large proportion of the variance in IBIs in the study population while the presence (or absence) of parasitic cysts on the mother during the interval explained a significant, but much smaller, proportion of the variance in IBIs. There is no significant interaction effect, i.e., no difference in the effect of maternal cysts on IBIs for mothers whose previous offspring did or did not die before they conceived their next offspring.

€ interbirth interval data ($n = 72$) were collected from a large number (47) of individual female geladas. Nearly 60% ($n = 28/47$) of these females contributed a single IBI to the analysis, with the rest ($n = 19$) contributing an average of 2.3 IBIs to the analysis (range 2–4 IBIs/female). Nearly 60% ($n = 11/19$) of the females contributing multiple IBIs to the analysis had IBIs in multiple categories (i.e., with cyst, without cyst, etc.).

* a dichotomous variable: previous offspring was deceased (1) or alive (0) when the subsequent offspring was conceived.

** a dichotomous variable: mother did (1) or did not (0) possess a parasitic cyst during the interbirth interval.

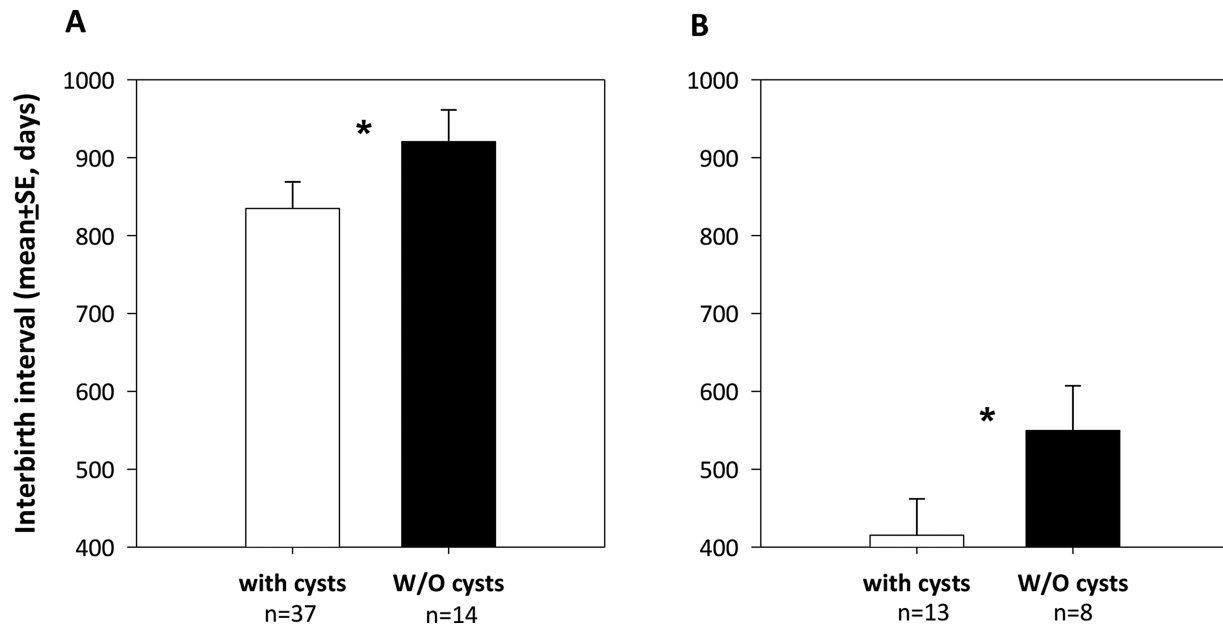


Fig. 4. Mean (\pm SE) interbirth intervals (IBIs) for females with and without parasitic cysts. Mothers with cysts exhibited IBIs that were \sim 3–4 months longer than those without cysts both among (A) females whose previous offspring was alive at the time they conceived their subsequent offspring and (B) females whose previous offspring died before they conceived their subsequent offspring. * = difference is statistically significant at $P < 0.05$ (see Table I). Numbers below the maternal classes represent the sample size of IBIs in each class.

DISCUSSION

Our study provides the first empirical evidence that disease associated with tapeworm infection can increase mortality and reduce fertility in wild nonhuman primate hosts. We found that larvae of *Taenia serialis* encyst in wild geladas at Guassa, Ethiopia, where one out of every six geladas in the study population possessed at least one cystic structure (coenurus) during the 6½ year study period. *T. serialis* coenuri negatively impacted gelada survival at Guassa, and this effect spanned at least two generations. Mortality was significantly higher for adult males and females with coenuri than for members of their sex without coenuri and offspring of females with coenuri suffered significantly higher mortality than offspring of healthy females. Moreover, adults with coenuri exhibited lower fertility than members of their sex without coenuri: females experienced longer interbirth intervals when they possessed coenuri than when they did not, and males with cysts rarely successfully usurped reproductive control over harems of fertile females from other males.

How Illness Associated with *Taenia* Infection Impacts Gelada Host Fitness

Our results demonstrate that *Taenia* coenuri affect several important host life-history traits for male and female geladas in ways that likely depress host fitness. Our results are consistent with findings

from several experimental studies of related helminths that have demonstrated the detrimental effects of these parasites on host survival and fertility in wildlife [reviewed in Tompkins & Begon, 1999; Tompkins et al., 2002]. Experimental reductions of parasite load enhanced survival in anthelmintic-treated red grouse [Hudson et al., 1992], snowshoe hare [Murray et al., 1997], and Soay sheep [Gulland, 1992] when compared to untreated conspecifics. Treatment with anthelmintics also resulted in enhanced breeding success for female red grouse [Hudson, 1986]. Although comparative experimental data for wild primates are not available, evidence from several studies suggests that during periods of food shortages, parasite infection is associated with mortality and population decline [e.g., Chapman et al., 2006; Chapman et al., 2007; Milton, 1996]. Understanding *how* parasites reduce fertility or increase mortality of host animals is also vitally important.

Many parasites affect host survival directly by causing pathology. Other parasites affect host fitness indirectly by increasing host susceptibility to predation or reducing host competitive fitness [Scott, 1988]. While we lack the necessary evidence to determine the exact mechanism by which taeniid parasitism reduces reproductive potential or accelerates death among geladas, gelada hosts may suffer disproportionately higher mortality as a result of parasite-associated changes in behavior (e.g., reduced mobility) or conspicuousness to potential predators [Scott, 1988]. Indeed, Guassa is home to

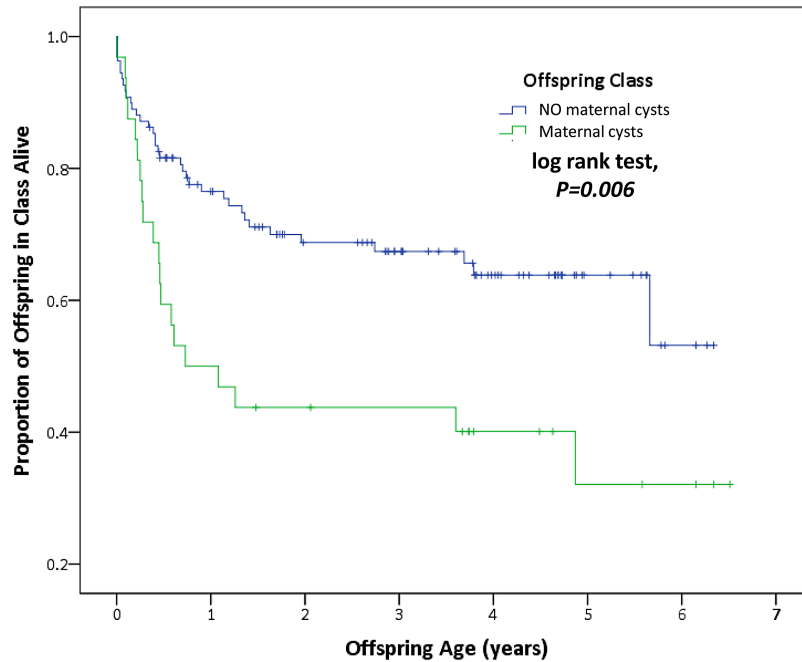


Fig. 5. The effect of maternal parasitic cysts on offspring survivorship. Offspring whose mothers did not possess a parasitic cyst at the time they gave birth (solid line, $n = 109$, 73 right censored) were significantly more likely to survive than offspring whose mothers had parasitic cysts (hatched line, $n = 32$, 12 right censored) (NOTE: In the Kaplan-Meier survival curves for both classes of offspring, hatch marks indicate the presence of right censored individuals [i.e., those offspring that are still alive as of the end of the study period, in July 2013]).

several species of predators of geladas, including hyenas and leopards. If a gelada at Guassa suffers from illness associated with *T. serialis* infection, and if that illness reduces the host's mobility (making it weaker or slower than healthy conspecifics), then the survival of that host may be compromised.

Parasite-enhanced vulnerability to predation (in intermediate hosts) can even help facilitate transmission of some parasites to their definitive hosts [Ewald, 1995; Hoogenboom & Dijkstra, 1987; Webber et al., 1987]. Although the definitive host of *T. serialis* at Guassa is, as yet, unknown, it is likely to be a canid whose feces disperses *T. serialis* eggs among the grasses, sedges, and forbs that dominate the grassland at Guassa and form the basis of the gelada diet at this site [Fashing et al., 2014]. While the adult stage of some *Taenia* spp. are highly host specific (e.g., both *T. saginata* and *T. solium* use humans as their sole definitive host), the adult stage of other *Taenia* spp. (including *T. serialis*) appear to be less host specific, relying on a variety of canids or felids as definitive hosts. Of the canids present at Guassa (Ethiopian wolves, cryptic African wolves, and domestic dogs), the critically endangered Ethiopian wolf is by far the most often found in close proximity to geladas [Venkataraman et al., in press], making it a likely candidate (but not the only candidate) definitive host for *T. serialis* at this site. In fact, Guassa is the only remaining Afroalpine habitat in Ethiopia where geladas and Ethiopian wolves (both endemic to Ethiopia) are known to regularly co-occur

and form mixed-species associations [Venkataraman et al., in press]. Even though Ethiopian wolves primarily hunt and eat rodents [Ashenafi et al., 2005; Sillero-Zubiri & Gottelli, 1995], which are likely *T. serialis*'s main intermediate hosts, they do occasionally scavenge the remains of deceased geladas at Guassa (Nguyen & Fashing, pers. obs.). Thus, by reducing the survivorship of its intermediate hosts, *T. serialis* can, in principle, increase its chances of being transferred (through scavenging or predation) from its intermediate to its definite host(s), thereby completing its development from larvae to sexually reproducing adults.

Host fitness can also be compromised as a result of parasite-associated changes in host competitive ability [Scott, 1988]. For males, access to fertile females is an important determinant of fitness [e.g., Clutton-Brock et al., 1982] and a reliable indicator of a male's access to females is his position in the male social hierarchy [Alberts et al., 2003]. However, parasites can reduce a male's ability to both assume and maintain his position in the male social hierarchy [e.g., Freeland, 1981; Rau, 1983, 1984]. Our finding that male geladas with *coenuri* very rarely ($n = 2$ of 35 takeover events) successfully assumed control over social units of adult females from other males suggests that at Guassa, parasites can compromise a male gelada's ability to obtain breeding opportunities. Male geladas with *coenuri* may be less physically able to challenge other males for leadership of one-male units, less likely to be

successful when they do so, or both. In gelada societies, leader males sire nearly all of the offspring [Snyder-Mackler et al., 2012], so competition for leadership positions (and the breeding opportunities they confer on leader males) is fierce, often resulting in injury, illness and even death (Nguyen & Fashing, pers. obs.). Reproduction is, however, not only dangerous, but also energetically expensive [Archie et al., 2014]. Energy that parasites usurp from host animals is energy these animals cannot spend on their own growth, development and reproduction [Moller, 1997]. Unfortunately for male geladas with coenuri, being energetically compromised appears to exact a heavy cost in terms of reduced mating opportunities, opportunities which might have resulted in offspring production.

In contrast to males, female fitness is less limited by access to mates than by ability to produce and rear offspring [Trivers, 1972]. Parasite-caused illness can not only reduce the total number of offspring a female produces during a given reproductive season [Saumier et al., 1986] or over her reproductive lifespan [Hawkins & Morris, 1978; Hope-Cawdery, 1976], it can also compromise her ability to rear young successfully [Weatherly, 1971]. Similarly, virally-caused illness can also negatively impact female reproduction. Female chimpanzees, for example, infected with simian immunodeficiency virus (SIV_{cpz}) at Gombe, Tanzania had fewer births and suffered higher infant mortality than uninfected females [Keele et al., 2009]. Our findings that female geladas at Guassa with coenuri took longer to give birth to their next offspring and experienced higher offspring mortality compared to mothers without coenuri suggest that, like female chimpanzees with AIDS-like immunopathology at Gombe [Keele et al., 2009], female geladas at Guassa with coenuri (and suffering from tapeworm infestation) have less ability to both produce and rear offspring compared to females without coenuri. Such ecologically-driven sources of intraspecific variability in fertility and offspring survival have the potential to exert major influences on lifetime fitness, especially for female members of species characterized by “slow” life histories (i.e., late maturation, long lifespans, and low rates of reproduction and offspring growth) for whom each act of reproduction is a potentially major contributor to lifetime fitness [Altmann & Alberts, 2003].

Why is *Taenia Serialis* So Virulent in Geladas at Guassa?

The magnitude of the tapeworm-related reductions in several fitness components among wild geladas at Guassa suggests that *T. serialis* is adopting a strategy of intense exploitation of geladas as an intermediate host. While some parasites exploit their hosts’ resources prudently, reproducing

slowly while ensuring long-term access to host resources, other parasites exploit their hosts’ resources more aggressively, reproducing rapidly at the risk of depleting their resource base precipitately [Frank, 1996; Poulin, 2007]. Because local conditions differ, each parasite population may evolve toward a level of host exploitation that is optimal for the conditions in its local host population and environment [Dybdahl & Storfer, 2003; Poulin, 2007].

From the host’s point of view, intense exploitation by parasites can often lead to high levels of virulence, defined as the amount of harm a parasite causes its host [Frank, 1996; Poulin, 2007]. Because infectious diseases exert major influences on the demography of animal and plant populations, understanding why some diseases are more virulent than others is a vitally important area of research [Anderson & May, 1982; Day & Proulx, 2004; Frank, 1996; Osnas & Dobson, 2012]. While recent research has challenged the earlier view that parasites evolve towards becoming harmless to their hosts [e.g., Day, 2003; Osnas & Dobson, 2012], we still know little about why some infectious agents inflict more harm on their hosts than others. Below, we provide two possible explanations for why *T. serialis* is adopting a strategy of intense exploitation of geladas at Guassa.

Parasites with complex life cycles (e.g., vector- or predator-borne parasites) sometimes employ different exploitation strategies for different hosts [Ewald, 1995; Poulin, 2007]. Current evidence indicates that among helminths with complex life cycles involving predation as a means of transmission, host exploitation (and virulence) is often highest in intermediate hosts and lowest in definitive hosts [Ewald, 1995; Poulin, 2007]. One explanation for these differences is that some parasites have evolved to use intermediate hosts as resource bases and definitive hosts as dispersal or transport agents [Ewald, 1995; Poulin, 2007]. If the parasite’s fitness is tied primarily to the mobility of its definitive host, selection should favor prudent exploitation of this host. In contrast, as the parasite’s resource base, the intermediate host should be exploited more intensely, especially if, by debilitating intermediate hosts, parasites also enhance their transmission success to definitive hosts via predation or scavenging [Ewald, 1995; Poulin, 2007]. The amount of harm *T. serialis* causes its definitive host(s) at Guassa is presently unknown, but, given the parasite’s exploitation of geladas, we would expect it to exploit its definitive host(s) more prudently than it does its intermediate host.

An additional, or alternative, explanation for *T. serialis*’s seemingly intense exploitation of geladas at Guassa may be related to superinfection, where more than one parasite infects an individual host [Alizon et al., 2013; Frank, 1996; Nowak & May, 1994]. All things being equal, when multiple (unrelated or distantly related) parasites co-infect a single host, selection would favor those parasites

that exploit the host's resources more rapaciously, which in a classic "tragedy of the commons" fashion [Hardin, 1968] would result in more rapid depletion of the parasites' shared, limited resource (i.e., the host) [Frank, 1996]. Perhaps geladas with coenuri represent those individuals that have become infected by some critical number of *T. serialis* parasites above which rapacious exploitation of hosts is more likely.

Superinfection may offer some clues as to why coenurosis is so virulent in geladas at Guassa, as well as why the disease is more prevalent in adults than immatures in this population. This latter pattern was also recently reported among geladas in the Simien Mountains [Schneider-Crease et al., 2013]. Age-dependent variability in the prevalence of coenurosis and other diseases can occur because of age-related variability in (a) innate or acquired immunity or (b) exposure to pathogenic agents among hosts [Woolhouse, 1998]. If immunocompetence, which improves with age and experience [Cattadori et al., 2005; Cornell et al., 2008], offers geladas protection against coenurosis, we would expect lower prevalence of this disease in older animals. Because we found the opposite pattern—higher prevalence of coenurosis in older geladas—we suggest that immune response is not very protective against tapeworms in geladas [c.f., Hayes et al., 2004; Maizels et al., 2004; Turner & Getz, 2010]. Age-related increases in prevalence could arise from (a) greater exposure to parasites ingested while foraging because of increases in the amount of food animals must consume as they progress toward adulthood [George-Nascimento et al., 2004; Morand & Harvey, 2000] or (b) greater accumulation of parasites in older hosts because of increasing opportunities to encounter and accumulate parasites over time [c.f., Cooper et al., 2012; Parr et al., 2013; Poulin & Morand, 2000]. The increased prevalence of coenurosis with age in geladas is consistent with the hypothesis that superinfection (arising from age-related increases in parasite exposure or accumulation) results in greater harm to afflicted hosts. To more fully test these ideas, however, will require additional information about parasite genetic diversity among and within host animals and populations.

Directions for Future Research: Population, Species and Ecosystem Level Impacts of *T. Serialis*

Our finding that *Taenia serialis* coenuri are pathogenic to gelada hosts at Guassa, Ethiopia suggests that some cestodes have the potential to exert substantial negative impacts on the health, reproduction and lifespan of nonhuman primate hosts in the wild. Parasites that can decrease the survival or reproduction of individual hosts have the potential to also affect the distribution or density of

host populations [Scott, 1988]. However, documenting the role of specific parasites in regulating the abundance of specific host populations can be extremely difficult to accomplish in field settings (where animals are exposed to many other selective pressures besides disease-causing organisms) [Hudson et al., 2002]. To date, a small number of experimental studies of natural helminth-host systems have found evidence that some parasites can regulate host population cycles (i.e., fluctuations in host population densities) in natural settings [e.g., red grouse in Scotland: Hudson et al., 1998].

Although experimental perturbations of host/parasite systems may be the best means of establishing parasite regulation of host populations [Scott & Dobson, 1989], such approaches can be impractical in vulnerable or protected animal populations. Further long-term monitoring of the gelada population at Guassa would provide additional data to enable researchers to evaluate whether *T. serialis* has the potential to play a significant role in regulating gelada host population dynamics at this site and elsewhere in the species' range. While longitudinal monitoring of individual animals in natural populations can be difficult to sustain [Clutton-Brock & Sheldon, 2010b], it can provide valuable data on individual- and population-level health status that can be used to make informed predictions about the future of vulnerable populations or species [Clutton-Brock & Sheldon, 2010a].

We suggest that *Taenia* parasitism could represent a serious threat to the conservation of remaining gelada populations since oscillations in population size can increase the likelihood of local extinction, especially if remaining populations are small and isolated from one another [Purvis et al., 2000]. At present, little is known of the status and distribution of geladas across their historic range [Gippoliti, 2010]. However, with <3% of the original Ethiopian Highlands habitat remaining [Williams et al., 2005], gelada abundance has undoubtedly declined dramatically over the past several decades with the cataclysmic loss of their primary habitat to farmland and grazing areas [Gippoliti & Hunter, 2008].

Finally, our findings raise the intriguing possibility that *T. serialis* may play an important role in shaping the structure and function of the ecological community in the threatened Ethiopian Highlands. The potential of some parasites to regulate the abundance of some host populations suggests that parasites may also modify the relative abundance of different hosts within a community, as well as the structure and function of ecological communities themselves [Minchella & Scott, 1991; Scott, 1988; Thompson et al., 2005]. Given that *T. serialis* likely exploits a variety of intermediate hosts besides geladas (including rodents, lagomorphs, ungulates, humans and their livestock) and one or more definitive hosts at Guassa and in other Ethiopian

Highlands ecosystems, the parasite may play a disproportionately large role in influencing the health and composition of the animal and plant communities where it occurs. Further research is urgently needed to determine the potential role that parasites—especially those like *T. serialis* that likely exploit a wide variety of host species—play in regulating the structure and function of threatened ecological communities.

ACKNOWLEDGEMENTS

We thank California State University Fullerton, Dean Gibson and San Diego Zoo, Margot Marsh Biodiversity Foundation, Pittsburgh Zoo, Cleveland Metroparks Zoo, Primate Conservation Inc., Gisela and Norman Fashing, Donna and Karl Krueger, Anita and Hans-Peter Profunser, and Christopher Schroen for their financial support of our research at Guassa. We thank the Ethiopian Wildlife Conservation Authority, Amhara Regional government, and Mehal Meda *Woreda* for permission to conduct this research. Zelealem Ashenafi provided valuable advice about working at Guassa and Badiloo Muluyee, Ngadaso Subsebey, Bantilka Tessema, Shoafera Tessema, Talegeta Wolde-Hanna, and Tasso Wudimagegn provided vital logistical support. We also thank Christiane Schwarz for assistance in the laboratory at DPZ, Nadine Schminke and Larissa Hummel for preparing the histological slides, and Paul Bechtold, Eva Gruber-Dujardin, and Franz-Josef Kaup for helpful discussions of the histopathological results. Lastly, we thank two anonymous reviewers for their valuable comments on this manuscript. Our research was entirely noninvasive and satisfied the legal requirements of Ethiopia.

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