Research Article



Gastro-Intestinal Parasites Co-Infection and their Interaction as Drivers of Host Heterogeneity in South African Communal Goat Populations

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Abstract | The study was conducted to evaluate how the concomitant infecting gastro-intestinal parasites (GIPs) modifies the intensity of infection, distribution pattern and host susceptibility to parasite within the South African communal indigenous goat population. A total of 288 goats were randomly sampled in different agro-ecological zones of South Africa. For each goat, the intensity of the GIPs was determined using a modified McMaster technique. Four subsets of data were used: the first included goats infected with single GIP species, either strongyles, Strongyloides papillosus, or Trichuris sp., the second, third and fourth considered goats co-infected with any two possible combinations of the three GIPs. The GLM procedures were used to analyse data. The three nematodes exhibited different ageintensity profiles. For single infections, infection intensity for strongyles and *Trichuris* sp., were higher (p<0.05) in young goats compared to other age groups. Co-infection by S. papillosus and Trichuris sp., strongyles and Trichuris sp. increased the infection intensity with the host age, but their pattern did not change (ρ >0.05). Strongyles intensity pattern in co-infection with either *S. papillosus* or *Trichuris* sp. did not change, as young goats exhibited higher (p<0.05) intensity than other age groups. The infection intensity for S. papillosus and Trichuris sp. between goat of different ages were similar (p>0.05) when co-infected with strongyles. Sex-intensity profile of all GIPs in single infections did not differ (p>0.05). Co-infection by S. papillosus and Trichuris sp. did not influence (p>0.05) the sex-intensity profile of these nematodes. Goats co-infected by strongyles with either S. papillosus or Trichuris, the intensity of these GIPs was high (p<0.05) in females compared to males. Multiple GIPs infections resulted in the accumulation of GIPs in the host population and variation in parasitism between goat ages and sexes. Concomitant GIP infections modify host susceptibility and influence heterogeneity amongst individual hosts.

Keywords | Age-intensity relationship, Strongyloides papillosus, Strongyles, Trichuris

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INTRODUCTION

astro-intestinal parasitism by a single species is an exception in veld conditions in ruminants (Cox, 2001; Telfer et al., 2010; Mpofu et al., 2020). The fact, until recently more or less ignored, is that most parasites co-exist with other parasites (Telfer et al., 2010; Thumbi

et al., 2014). Furthermore, parasites that concurrently infect a host may interact with each other, especially those occupying the same niche area within their host might change their respective niches, consequently, they may eventually be able to co-exist (Poulin, 2007; Cattadori et al., 2008). Interactions between organisms, whether direct or indirect, are important in determining the community

structure and bringing forth biodiversity (Bonsall and Hassell, 1997). In the parasite communities infecting livestock populations, direct interactions may arise when these parasites compete for common resources, such as food or space (Lello et al., 2004; Mideo, 2009), however, the population size of either or both pathogens involved may be limited as a result (Petney and Andrews, 1998). Notably, depending on which other gastro-intestinal parasites (GIPs) present in the gastro-intestinal tract of an animal, notably, the attachment sites of these GIPs may vary significantly (Ellis et al., 1999; Vaumourin et al., 2015). The indirect interactions may occur by modifying the host's immune response (Cattadori et al., 2007; Jolles et al., 2008) or susceptibility to the second or other parasite species infection (Holmes et al., 1974; Mackenzie et al., 1975). Interactions between concomitant parasites may also alter the outcome of the subsequent infection, such as by minimizing or prolonging prepatent times (Kaufmann et al., 1992; Gale et al., 1997), or by increasing pathogens pathogenicity (Kaufmann et al., 1992; Goossens et al., 1997; Petney and Andrews, 1998).

Environmental factors may influence the transmission or reproductive rate of one parasite over the other (Petney and Andrews, 1998; Altizer et al., 2006; Ezenwa and Jolles, 2011), interactions between various parasites might determine how climatic conditions affect host-parasite dynamics of an individual. Within the host, parasites that concurrently exist may have a synergistic or antagonistic interaction that may determine important repercussions on animal health (Cattadori et al., 2008; Ezenwa et al., 2010) attributed to the fact that they could modify the epidemiology, infection duration of other several parasites, and host susceptibility and thus treatment and control measures. The relative incidence of a particular infection induced by one parasite can intensify the risk of exposure to a second parasite (Karvonen et al., 2009), even though the interactions within the host are antagonistic. The host behaviour, environmental factors, infection history, and pathology influence the interactions between the parasites (Poulin, 2007; Behnke, 2008; Telfer et al., 2008), complexifying the interactions whether it influences between-host or within-host mechanisms (Hawley and Altizer, 2010).

In natural grazing systems, goats are commonly co-infected with multiple GIPs (Ntonifor et al., 2013; Tsotetsi et al., 2013; Verma et al., 2018; Mpofu et al., 2020). Noteworthy, the prevalence of different GIPs has been well recorded including South Africa (Tsotetsi and Mbati, 2003; Gwaze et al., 2009; Mpofu et al., 2020) and other African countries (Odoi et al., 2007; Ntonifor et al., 2013; Zvinorova et al., 2016). The GIPs are regulated by an acquired immune response, depicted by a type III response or convex ageintensity relationship (Hudson et al., 2006; Cattadori et al.,

2008) as a response to the historical exposure to parasites (Woolhouse, 1992, 1998). This age-intensity curve is substantially illustrated by simulations describing the development of the immunity acquired as a consequence of the cumulative exposure to the infective stages of the parasite (Woolhouse, 1992, 1998). Immune-mediated species interactions may determine the susceptibility variability and rate of infection amongst hosts and thus, determine the host population's parasite community (Andreansky et al., 2005; Graham et al., 2005; Thorburn et al., 2006; Cattadori et al., 2007, 2008). This type of competition result because of the negative interaction between the two parasite species, not due to competition for resources (food and space) but attributed to a common predator (Holt, 1977; Bashey, 2015).

Despite growing attention in parasite co-infections, surprisingly, very few studies have evaluated the factors that be accredited for observed GIPs co-infection and their interactions in goats. The challenge is that co-infections or multi-parasitism is complex to describe, in particular, detecting interaction among associations (Keesing et al., 2010), particularly in the natural systems (Lello et al., 2004; Fenton et al., 2014) since the rate of possible interactions increases with the number of considered parasites (Petney and Andrews, 1998). Therefore, it is more pertinent to investigate the GIPs infections in the context of the comprehensive pathogenic neighbourhood of the host since each parasite eventually contributes to the clinical outcome and prediction of the infection in the individual host. Therefore, this study was conducted to determine how the concomitant infecting GIPs modifies the intensity of infection, distribution pattern and host susceptibility to parasite within the South African communal indigenous goat populations with respect to age and sex of goat, sampling season and agro-ecological zone.

MATERIALS AND METHODS

ETHICAL APPROVAL

This study was approved by the Animal Research Ethic Committee of the Faculty of Science, Tshwane University of Technology (FCRE 2017/10/01 (02) (SCI)). Ethical concerns were considered by adhering to the South African animal welfare regulations and practices, and experiments were adapted to the ethical guidelines for animal usage in research of Tshwane University of Technology, South Africa. Written informed consents were obtained from the communal farmers from which study samples were collected.

THE PARASITE-HOST SYSTEM

A longitudinal study was carried, wherein the parasite and host data were obtained from a population of 288 communal indigenous goats randomly sampled in different agro-ecological zones (arid, semi-arid, dry sub-humid and humid) of South Africa. The selected agro-ecological zones vary in the percentage of the land surface, rainfall distribution and length of the growing period, aridity index and vegetation type (Table 1). Ear tags (Allflex® - Somerset West, Western Cape, South Africa) bearing individual identification numbers were placed on the right ear of each animal during the initial sample collection in order to allow for repeated sampling of the same animals over the study period. The animals were kept under extensive grazing systems where during the day they were released to graze on communal lands and kraaled at night. The flocks were classified by age: adult (>2 years), young goat (1-2 years) and suckling kids (<1 year) as described by Kheirandish et al. (2014).

SAMPLE COLLECTION AND ANALYSES

For each goat, about 10 g of fecal sample was obtained directly from the rectum and placed into airtight containers and labeled. Samples were collected twice during each season from each of the animals. Samples were maintained in cooler boxes between 2-4 °C prior and later refrigerated prior to analyses and transported to the laboratory for further coprologic examination within 24 h. The intensity measured by the fecal egg count (FEC) of the three nematodes, Strongyloides papillosus, strongyles, and Trichuris sp., for each goat, were determined using modified McMaster technique as described by Hansen and Perry (1994) in the positive fecal samples, and the slides were prepared for examined under a microscope (x10). The floatation fluid used was NaCl. Eggs of different GIPs were identified based on their sizes and morphological features (Foriet, 1999; Zajac and Conboy, 2006). The fecal samples were grounded into five drops of bloat guard to prevent bubbles when counting, egg count was multiplied by 100 to give an estimation number of eggs in the animal system (Aumont et al., 2003). The intensity of the other two GIPs, Eimeria and Moniezia sp. were also quantified but goats co-infected with these GIPs were excluded from the current study as very few animals were coinfected with these parasites.

STATISTICAL ANALYSIS

Four sets of data were used: The first comprised goats infected with single GIP species, either *S. papillosus*, strongyles or *Trichuris* sp., the second, third and fourth comprised of goats co-infected by any two possible combinations of the three nematodes. The FEC's for all GIP found were transformed through a base 10 logarithm (log₁₀FEC+25) to approximate a normal distribution. The transformed data were used for statistical analysis. The General Linear Model (GLM) procedures of MiniTab 17 were used to examine the GIPs intensity as a function of host characteristics (age and sex), agro-ecological zone, season and infection type. The FEC transformed data and

the results were then back-transformed by taking antilogarithms and presented as geometric means (GFEC). Means were separated using Fisher's Protected LSD test (ρ <0.05).

RESULTS

The effect of sex of the goat on the single and dual coinfection intensities for S. papillosus, strongyles, and Trichuris sp. is presented in Table 2. The single infection intensities in male and female goats for S. papillosus, strongyles and Trichuris sp. were significantly similar (p>0.05), however, in dual co-infections for strongyles and S. papillosus, strongyles and Trichuris sp., the intensities were significantly higher (p<0.05) in females than in males, whilst the intensity for those co-infected with strongyles and Trichuris sp. remain significantly similar in both sexes.

The effect of sampling season on the single and dual co-infection intensities for S. papillosus, strongyles, and Trichuris sp. is presented in Table 3. The single infection intensities in winter and summer sampling seasons in South African communal goat populations for S. papillosus and Trichuris sp. were significantly similar (p>0.05), whilst that of strongyles was significantly different (p<0.05). However, in dual co-infections for Trichuris and either S. papillosus or strongyles, the Trichuris intensity remained significantly similar (p>0.05) in both seasons. Goats co-infected with strongyles with either S. papillosus or Trichuris exhibited higher (p<0.05) strongyles intensity in winter compared to summer sampling season. In any of the co-infections for S. papillosus, goats exhibited similar (p>0.05) intensity of S. papillosus in both seasons.

The three nematodes exhibited different age-intensity profiles: S. papillosus intensity remained significantly constant (p>0.05) with increasing host age, while the strongyles and Trichuris sp. intensity exhibited a significantly (ρ <0.05) type III convex age-intensity relationship (Table 4). The intensity of the GIPs understudy increased numerically from a single infection to any dual co-infection. The strongyles intensity pattern in single infection and dual co-infection with S. papillosus and Trichuris sp. did not change, as young goats exhibited higher (p<0.05) intensity than other goats, whilst, that of neither S. papillosus and *Trichuris* sp. the intensity pattern was similar (p<0.05) between goats of different ages in co-infection. Goats of different ages co-infected with S. papillosus and Trichuris sp. exhibited similar (p>0.05) intensities. However, their pattern of intensity changed wherein in single infection, the young goats exhibited higher Trichuris sp. intensity but in S. papillosus co-infection the intensity was similar (p>0.05).



Table 1: Agro-ecological zones and their features in South Africa.

| Agro-ecological zone | - Annual Rain- fall (mm) | Length of Growing Period (d) | Aridity in- dex* (P/Ep) | Percentage of land surface | Vegetation type | % range- land | % culti- vated |
|----------------------|-----------------------------|------------------------------|----------------------------|----------------------------|------------------------------------|------------------|-------------------|
| Desert | < 200 | | | 22.8 | | | |
| Arid | 201–400 | <90 | <0.39 | 24.6 | Annual grassland | 87 | 7 |
| Semi-arid | 401–600 | 90-179 | 0.40-0.79 | 24.6 | Thorny savannahs | 54 | 35 |
| Dry sub-hu- mid | 601–800 | 180-269 | 0.80-0.11 | 18.5 | Broad-leaved savannah woodlands | 34 | 47 |
| Humid | 801-1000 | 270-365 | >0.12 | 6.7 | Rain forest and savannahs | | |
| Super humid | >1000 | | | 2.8 | | | |

^{*} The ratio of precipitation to potential evapo-transpiration; Adapted from Schulze (1997); Mpofu et al. (2017); UN, Environment Management Group (2011); Reynolds et al. (2007).

Table 2: Mean GFEC intensity (±SE) of different gastro-intestinal parasites single and co-infections with respect to sex of goat.

| Sex of | Si | ingle infection | ections Dual co-infections | | | | | | |
|--------|-------------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|-------------------------------|-----------------------------|
| goat | goat Strongyles S. papillosus | | Trichuris | Co-inf | ection 1 | Co-info | ection 2 | Co-infe | ection 3 |
| | | | sp. | Strongyles | S. papillosus | Trichuris sp. | S. papillosus | Trichuris sp. | Strongyles |
| Male | 199.54 ^a ± 26.47 | 125.63 ^a ± 26.34 | 130.58 ^a ± 26.39 | 313.87 ^b ± 26.24 | 271.59 ^b ± 26.26 | 282.59 ^a ± 28.25 | 221.58 ^a ± 26.21 | 229.90 ^b ± 26.25 | 453.14 ^b ± 26.20 |
| Female | 257.25 ^a ± 26.44 | 126.97 ^a ± 26.32 | 124.12 ^a ± 26.36 | 599.50 ^a ± 26.25 | 432.90 ^a ± 26.27 | 190.76 ^a ± 27.03 | 252.57 ^a ± 26.11 | 369.61 ^a ±26.28 | 867.91 ^a ± 26.17 |

 $^{^{}a,b}$ Column means with different superscripts differs significantly (p<0.05).

Table 3: Mean GFEC intensity (±SE) of different gastro-intestinal parasites single and co-infections with respect to sampling season.

| Sampling | Sir | ngle infectio | ns | | | Dual co | -infections | | |
|----------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|
| season | Strongyles | S. papillo- | Trichuris | Trichuris Co-infection 1 | | Co-ii | nfection 2 | Co-infection 3 | |
| | sus | | sp. | Strongyles | S. papillosus | Trichuris | S. papillosus | Trichuris | Strongyles |
| Winter | 292.42 ^a ± 26.44 | 126.00 ^a ± 26.32 | | 587.00 ^a ± 32.94 | 367.88 ^a ± 26.25 | 238.88 ^a ± 27.78 | 252.57 ^a ± 26.18 | 382.18 ^a ± 26.25 | 990.40 ^a ± 30.88 |
| Summer | 167.43 ^b ± 26.42 | 126.48 ^a ± 26.30 | 127.57 ^a ± 26.35 | 322.71 ^b ± 26.22 | 335.72 ^a ± 26.24 | 216.32 ^a ± 27.10 | 221.58 ^a ± 26.12 | 245.81 ^a ± 32.94 | 326.24 ^b ± 31.02 |

^{a,b} Column means with different superscripts differs significantly (p<0.05).

Table 4: Mean GFEC intensity (±SE) of different gastro-intestinal parasites single and co-infections with respect to goat sex.

| Age of | Single infections Dual co-infections | | | | | | | | |
|----------|--------------------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|------------------------------|-----------------------------|-----------------------------|
| goat | Strongyles | S. papillosus | Trichuris | Co-inf | ection 1 | Co-in | fection 2 | Co-infection 3 | |
| | | | sp. | Strongyles | S. papillosus | Trichuris | S. papillosus | Trichuris | Strongyles |
| Suckling | 166.99 ^b ± 26.68 | 124.89 ^a ± 26.49 | 131.97 ^b ± 26.56 | 310.81 ^b ± 26.53 | 245.18 ^a ± 26.49 | 220.95 ^a ± 31.22 | 208.90 ^a ± 26.34 | - | - |
| Young | 576.13 ^a ± 26.84 | 126.93 ^a ± 26.59 | 424.65 ^a ± 26.68 | 500.97 ^a ± 26.37 | 231.89 ^a ± 26.34 | 282.88 ^a ± 28.07 | 241.71 ^a ± 26.19 | 255.85 ^a ± 26.28 | 853.72 ^a ± 26.38 |
| Adult | 148.43 ^b ± 26.37 | 127.53 ^a ± 26.27 | 129.58 ^b ± 26.31 | 355.33 ^b ± 26.15 | 280.04 ^a ± 26.14 | 195.11 ^a ± 28.90 | 234.00 ^a ± 26.244 | 340.02 a ± 26.12 | 461.53 ^b ± 26.07 |

^{a,b,c} Column means with different superscripts differs significantly (p<0.05).

The effect of the agro-ecological zone on the single and dual co-infection intensities for strongyles, *S. papillosus*, and *Trichuris* sp. is presented in Table 5. The single infection

intensities in different agro-ecological zones in South African communal goat populations for strongyles and *Trichuris* sp. were significantly similar (*p*>0.05). Goats in

humid zone exhibited a higher (p<0.05) single infection of *S. papillosus* compared to those in other agro-ecological zones. Goats in the humid and semi-arid zone with the co-infection of *Trichuris* with *S. papillosus* exhibited higher (p<0.05) *Trichuris* sp. intensity compared to those in other zones, whilst those in arid were having low infection

intensity. However, in dual co-infections for *Trichuris* and *S. papillosus*, the *Trichuris* sp. intensity was significantly higher (p<0.05) for goats in the humid zone compared to those in other zones. In goats co-infected with strongyles. with *S. papillosus*, the intensity of these GIPs was significantly similar (p>0.05) across the agro-ecological zones.

Table 5: Mean GFEC intensity (±SE) of different gastro-intestinal parasites single and co-infections with respect to agro-ecological zones

| Agro-eco- | Si | ngle infection | 18 | | Dual co-infections | | | | | |
|------------------|-----------------------------|-------------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|------------------------------|-----------------------------|--|
| logical zones | Strongyles | S. papillosus | • | Co-infection 1 | | Co-infection 2 | | Co-infection 3 | | |
| | | | | Strongyles | S. papillosus | Trichuris | S. papillosus | Trichuris | Strongyles | |
| Arid | 169.17 ^a ± 26.72 | 125.75 ^b ± 26.51 | 128.61 ^a ± 26.59 | 357.42 ^a ± 26.25 | 240.76 ^a ± 26.27 | 130.40° ± 28.91 | 248.20 ^a ± 26.24 | 288.58° ± 26.41 | 279.68 ^b ± 26.28 | |
| Semi-arid | 257.48 ^a ± 26.06 | 125.36 ^b ± 26.43 | 125.75 ^a ± 26.49 | 339.77 ^a ± 26.51 | 220.27 ^a ± 26.56 | 348.42 ^b ± 33.63 | 206.18 ^a ± 26.41 | 489.44 ^a ± 26.34 | 586.08 ^a ± 26.23 | |
| Dry sub-humid | 192.31 ^a ± 26.59 | 125.97 ^b ±26.42 | 127.43 ^a ± 26.48 | 388.71 ^a ± 26.20 | 294.51 ^a ± 26.24 | 251.53 ^b ± 28.36 | 311.67 ^a ± 26.36 | 335.32 ^b ± 26.31 | 333.86 ^b ± 26.23 | |
| Humid | 145.11 ^a ± 26.70 | 328.65 ^a ± 26.49 | 129.56 ^a ± 26.57 | 328.59 ^a ± 26.31 | 258.83 ^a ± 26.37 | 668.76 ^a ± 30.10 | 206.18 ^a ± 26.30 | 405.55 ^{ab} ± 26.34 | 487.85 ^a ± 26.25 | |

^{a, b, c} Column means with different superscripts differs significantly (p<0.05).

DISCUSSION

The observed convex age—intensity relationship or a Type III response in the intensity for strongyles and *Trichuris* sp. in the present study depicts that these two parasites are regulated by an acquired immune response. These findings are in concordance with earlier reports where the Type III convex-age intensity profile was observed in small ruminants (sheep and goat) (Sharma et al., 2009; Ayaz et al., 2013; Zvinorova et al., 2016). Noteworthy, Cattadori et al. (2007) postulated that if the host is infected by two parasites, the primary species immune-regulated and the second that can potentially reduce resistance to the primary, therefore the age—intensity profile of the primary species will be altered.

The strongyles are of high fecundity and transmission rate compared to other GIPs (Dabasa et al., 2017; Mpofu et al., 2020), consequently, it is no surprise that strongyles co-infection with either S. papillosus or Trichuris sp. leads to an overall higher strongyles infection intensities. The reason for higher strongyles and Trichuris sp. intensities in young goats with dual co-infection is evident. One possibility could be that such individuals are the most susceptible animals compared to other individuals and that in the presence strongyles, their immune response to both parasites is less efficient, attributed to immunological immaturity (Asanji and Williams, 1987; Mpofu et al., 2020) and weaning stress (Verma et al., 2018). Notably, the poor host condition may facilitate infection with strongyles (Hansen and Perry, 1994; Zajac and Conboy, 2006; Dabasa et al., 2017). A further logical explanation might be the

positive effect of substances produced by the strongyles which can positively or negatively induce changes in the gastric movement that can promote the passage of the *Trichuris* sp. to the small intestine, however, the evidence is insufficient to support such claims. A similar phenomenon had been observed when animals are co-infected with the *Trichostrongylus retortaeformis* and *Graphidium strigosum*, wherein it was postulated that the *G. strigosum* could promote the passage of *T. retortaeformis* into the small intestine (Cattadori et al., 2008).

The competition scenarios investigated in this paper should thus be common in nature. Our present results indicate that the competition between the species of GIPs is severe and therefore, has significant implications on numerous levels. Firstly, these findings reveal that the co-infection can modify the behaviour of the parasite community and its outcomes on the host. Secondly, the suppression may alter the epidemiology and/or fecundity patterns because it modifies the relative and absolute GIP load in the host. The elevated relative population size of the parasites within a host may increase the transmission risks, however, this phenomenon had been observed in different viruses affecting ruminants (Balmer et al., 2009). In the present study, co-infections seemed to enhance the heterogeneity of the GIPs between host and changed the level of parasite aggregation, however, a similar pattern was also observed in the rabbit population (Cattadori et al., 2007, 2008). The observed constant intensity infection by the S. papillosus in both single and co-infection status with any of the other GIPs indicates no discernible immune regulation. These differences could also be attributed to other developments,

which could produce such relationships, especially for *S. papillosus*. If the first parasite infection is not controlled by immune systems, then the age-intensity profile will not alter obviously, provided all other variables remain constant (Cattadori et al., 2007, 2008).

The season, agro-ecological zone, age, and sex also played a significant role in determining the co-infection pattern, particularly for strongyles and likely their role was somewhat brought about by the immune response. The observed aggregation and intensity of strongyles, S. papillosus and Trichirus sp. in female host animals was higher in comparisons to male host animals when coinfected with strongyles and S. papillosus, strongyles and Trichirus sp., but the results suggest that host characteristics and possible exposure shifts seem to be critical for to these parasites dynamics (Hudson et al., 2006). The observed aggregation and intensity of strongyles, S. papillosus, and *Trichirus* sp. depict that the presence of one parasite causes immuno-suppression (Behnke et al., 2001; Cox, 2001) during the winter season and in the female host animals than in the summer and male host animals. The immunesuppressive effect of strongyles was evident, consequently resulting in an increased infection intensity in both sexes of goats, but reduced the aggregation of other GIPs in coinfection, such that there were more goats diagnosed with S. papillosus and Trichirus sp. that also carried the strongyles. Brown et al. (2008) are of a view that the immunemediated competition benefits the pathogens that are able to escape the immunity by concealing from or being resistant to its effects. The findings that there is increased biasness in parasitism between sexes in co-infected goats in comparison with single species-infected goats postulates that female goats undergo hormonal immuno-suppressive and physiological changes that may in turn influence the GIP intensities (Sharma et al., 2009; Dabasa et al., 2017).

The production and/or an increase in molecules strengthening the immunity such as interleukins and antibodies may result if the parasites interfere with the host's immune system (Vaumourin et al., 2015). Immunity developed against specific parasite can protect the host against other parasites which are antigenically similar to the primary parasite, this is referred to as cross-immunity (Vaumourin et al., 2015), which could be the case in the results of this study as the presence of one parasite increases the aggregation and intensity of the other parasite in coinfection. This phenomenon had also been observed in rabbits infected with different GIP (Cattadori et al., 2007, 2008). Noteworthy, resistance to one GIP species could be coupled with resistance to the second or even the third GIP species (Gruner et al., 2004; Behnke et al., 2006). How different mechanisms of within-host competition between concurring parasites sharing the same niche affect each other remains unclear (Alizon et al., 2013; Bashey,

2015; Vaumourin et al., 2015).

CONCLUSION RECOMMENDATIONS

AND

Host heterogeneities could be brought by the changes in host susceptibility and exposure to the GIPs. Multiple GIPs species infections resulted in the accumulation of GIP infection intensity in the host population but also resulted in variation in parasitism between goat ages and sexes. The need to discuss how different and co-occurring parasites affect the health of goats is becoming abundantly clear. Particularly, to such an extent, the broad approach is challenging, particularly acknowledging the difficulties of accurately interpret such interactions because the range of possible interactions increases with the number of GIPs in question. Such challenges could be overcome with the multi-disciplinary collaboration studies and considering that the progress of such a wide method might primarily require refined data.

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AUTHORS CONTRIBUTION

This paper forms the part of the work toward the Ph.D. thesis of the first author TJM, under the guidance of KAN and BM. TJM designed the study, collected and analysed the data, and wrote the manuscript. KAN and BM designed the study, coordinated the work, and revised the manuscript. HG designed the study and revised the manuscript. All authors read and approved the final manuscript.

CONFLICT OF INTEREST

The authors have declared no conflict of interest.

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