Climate variations and the environmental population of gastrointestinal nematodes of ruminants

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HIGHLIGHTS

• Humidity and temperature are the main variables that affect the infective form migration behavior.
• The movement of larvae is random when humidity and temperature are adequately available.
• Fecal mass can serve as an important reserve for infective juveniles even during prolonged periods of drought.
• Different species of parasitic nematodes may present different biological characteristics that make their movement in the pasture microclimate easier or more difficult.

ABSTRACT: One of the major challenges facing beef cattle farming in Brazil, with the current situation of inefficacious anti-helminthic treatments and the absence of any prospect for new molecules appearing on the market, is sustainable control for gastrointestinal verminosis. The proposals currently being studied and those already evaluated show that the most coherent way in which to control gastrointestinal nematodes efficiently is by understanding their biology more thoroughly. There should be an emphasis on the free-living phases observed in the pasture microhabitat, which is directly influenced by climatic factors, among which temperature and humidity stand out. To a lesser degree, barometric pressure, solar ray incidence, cloud cover, evaporation, wind, quantity of vegetation and some other factors may interfere directly in their migration, survival and maintenance and, consequently, influence the rate of infection. The isolation of each environmental variable to determine its level of interference in the behavior of larvae in the pastures under field conditions is a practice that has not so far been accessible. Knowledge about climatic variations may be used as an important tool in the correct implementation of control strategies that aim to make intelligent use of anti-helminthic treatments, reducing the risk of animal infection and increasing the number of parasites in refugia. However, new field studies are still necessary to clarify the real contribution that each climate variable makes to the behavior of larvae in the pasture and their impact on the increased risk of infection and animal parasite burden.

Keywords: epidemiology, verminosis, microclimate, anti-helminthic, pasture, bovines.

Cite as

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INTRODUCTION

Gastrointestinal verminosis is a parasitic disease that affects cattle mainly in its subclinical form[1]. In most cases, therefore, the damage is only noticed in a loss in yield[2-5].

Environmental characteristics, especially related to the pasture microclimate, may directly affect the quantity of gastrointestinal nematodes (GINs) in the pasture environment and may raise the rate...
of infection. In tropical regions, such as Brazil, the climate is favorable to livestock production, but unfortunately the same environmental conditions that favor cattle farming also help infective nematode larvae to live and multiply all year round.

Currently, with the scenario of anti-helminthic resistance that can be observed worldwide, it is imperative to use all the information available to determine the most appropriate moment for the use of these treatments. Thus not only the parasite forms (present in the animal) but also the free-living forms (present in the pasture) can be suitably controlled.

Although the quantification of infective larvae in the pasture is limited to use in the field, given its practical applicability and the need for trained labor, this information is important in experimental studies to understand the population dynamics of trichostrongyloid parasites. Thus, understanding the epidemiology of GINs and the factors that affect the survival, movement and development of their larvae in the free-living phase can be the departure point for the development of sustainable programs to control verminosis.

These factors can be influenced directly by the climate[13], as occurs for rain, temperature, humidity, barometric pressure, sunlight, cloud cover, wind and quantity of vegetation[17], as well as by effects coming from birds, fungi and wild mammals. These conditions are highly variable and can change annually[18]. Based on data observed by Honer & Bianchin[19], in Brazil, a country in which climate conditions are very well defined, with hot wet summers and cool dry winters, environmental contamination by infective larvae generally reaches maximal levels in the wet season. In the dry season, the surviving helminth population is almost exclusively in the host, because at this time the conditions for maintaining the free-living phases in the environment are unfavorable, and the rate of larval movement is jeopardized. However, Soares[13,18] in Rio de Janeiro and Amarante et al.[20] in São Paulo indicate that the dry season does not have a negative influence on the development, survival and dynamics of nematode L3 (infective form) dispersal in pasture. This assertion is also corroborated by results seen by van Dijk & Morgan[21], when reporting that L3 do not need free water to migrate through grass. These different results show that, due to a wide variety of factors related to the environment, host and parasite in various studies, even those with similar methodology, the result observed could be the consequence of specific alterations in each study, being them methodological or environmental. These can have a very strong influence, to the point of affecting the complete experimental result.

It is therefore possible that in certain situations the variables influence the rate of distribution or survival of infective larvae in the pastures, such as when high precipitation and temperatures do not occur with the intensity and frequency expected during summer. This reduces the larval recovery rate in periods when they should in theory be high, which can at least partly explain discrepancies in results, such as high larval recovery rates in dry periods and low rates in rainy periods. This characteristic reinforces well established opinions on the dynamics of larval migration in the pasture environment, showing that alterations in larval density in the environment occur simultaneously with meso-variations (variations of the macroclimate)[6, 15, 16] and microclimatic variations (restricted to the environment where the larvae are located in the free-living phase). Among these variations, greater weight has been attributed to temperature and humidity[6, 15, 16].

The objective of this study was to compile the information available from the literature that relates to the epidemiology of bovine gastrointestinal verminosis, emphasizing the factors that influence survival, movement and development in free-living phases of GINs in the pasture microhabitat. These concepts supply an important basis on which to establish control strategies directed to environmental management and, consequently, to control in the animal. They may foster the correct, intelligent and sustainable use of anti-helminthic treatments, in order to reduce the pressure of selection for parasite resistance and to prolong the useful life of the anti-helminthic formulations that are most widely used in the field.

**Biological control of gastrointestinal infective larvae of ruminants**

For some time the almost exclusive and indiscriminate use of anti-helminthic treatments has been known to lead to greater parasite resistance and has increased the demand for organic or green products[17]. In these circumstances, various studies have sought new alternatives for the efficient and sustainable control of gastrointestinal verminoses with or without minimal usage of anti-helminthics, reducing the adverse effects in humans (from residues) and delaying the development of parasite resistance.

Among the main non-chemical control alternatives that have been evaluated until now, biological control is the method that stands out. As a rule, all animal species are regulated by other living
organisms (by antagonism) that are not manipulated by humans, instead occurring naturally. This may be denominated “natural biological control”. These living organisms, such as viruses, bacteria, fungi, protozoans, coprophagous beetles, worms, insects and ticks, are capable of reducing the quantity of GINs at the free-living stage and, as a consequence, naturally reduce environmental contamination by infective larvae. Normally, the term “biological control” describes the situation in which humans try to use naturally antagonist organisms against the parasites of domestic animals to reduce the population. However, only a small number of these organisms have shown promise in reducing the quantity of parasitic helminths in the environment and which, indirectly, influence the animal parasite burden.

Recently, various studies using nematophagous fungi have been carried out and produced promising results. However, other organisms such as coprophagous beetles and worms (Pontoscolex corethrus) have been identified less clearly and may have a direct effect on the availability of infective larvae in pastures, by means of degradation of the fecal pat and increase the free-living phases, those located mainly in the pasture, in which control tools are directed towards the parasitic stages, within the host. Biological control instead targets the free-living phases, those located mainly in the pasture and, for this reason, its use is reflected, initially, in a reduction in environmental contamination, and not directly in the animal parasite burden.

Most nematophagous fungi produce traps such as constrictive or non-constrictive rings and hyphae, buds, branches or sticky nets throughout the vegetative system of the hyphae. Some species, such as Arthrobotrys robusta and Monacrosporium thaumasium (Drechsler) de Hoog & Oorschot, it is essential that the nematophagous fungus should have the capacity to survive in storage and not cause damage to the ecosystem. These characteristics are extremely important and, when aggregated, they make these species highly efficient in combating free-living forms of life of gastrointestinal nematodes.

The greatest challenge today, is the large-scale production of economically viable nematophagous fungi that are easy to apply, efficient and meet the needs of industry to export this technology commercially. However, it is important to highlight that there are differences regarding regional epidemiology, which can occur within and between countries and depends, for example, on different climatic and management conditions and production systems, etc. Therefore, in ideal conditions for the development of free-living phases, biological control may not be enough, and thus other types of intervention are employed to prevent high levels of exposure of infective larvae in the pasture, which will consequently lead to clinical or subclinical parasitism in animals raised in the field, being a constant challenge.

The fungi inhabit a wide variety of substrates, such as soil, hummus and manure, and they can naturally influence the mortality rate of larvae and/or eggs, as soon as these are deposited in the environment. Some species, such as Pochonia chlamydosporia (Goddard) Zare & Gams, parasitize helminth eggs (the ovioidal effect), other species, such as D. flagrans, produce traps that evolve and kill the recently hatched larvae, and thus promote biological control in the pasture environment which, in many cases, may make it unnecessary to use anti-helminthic treatments. However, the efficiency of these organisms in the biological control of ruminant parasite helminths may often vary. This has been shown by Araújo et al., in Brazil, in a study that reported that M. thaumasium, when administered orally in bovines, reduced the quantity of infective larvae by about 100%. Assis et al., also in Brazil, observed that D. flagrans was more efficient in reducing the quantity of infective larvae of GINs in the pasture than was M. thaumasium, showing a reduction of 56.67% and 47.8%, respectively, when both were compared with the control group. Epe et al., in Germany, observed no significant difference in the number of eggs on faeces of sheep and in the L3 count in the pasture after treating sheep with D. flagrans, evidencing an absence of clear effects on GINs from this species of fungus. Faessler et al., in Switzerland, noted that the administration of D. flagrans in sheep did not reduce the egg count in faeces, but reduced environmental contamination by infective larvae and occasioned a suppression in the development of larvae in coproculture, during the period in which fungi were being fed.

All in all, the control of gastrointestinal verminosis using fungi with nematocidal activity has the potential, in the near future, to become a key part of the integrated control strategy against parasitic helminths of productive livestock. Biological control may not induce complete suppression of the
larval population in the environment, but it can make reductions that are sufficient to prevent adverse effects in the field\(^\text{[37]}\).

Unfortunately, not enough is yet known about the complex biological systems of these organisms that are natural antagonists of parasitic helminths of ruminants, which restricts the interest shown by industry in developing biological products to combat gastrointestinal verminosis\(^\text{[18]}\). Therefore, the integration of parasite control methods that are practical and financially significant is still the best alternative for controlling this issue in a sustainable and long-term way.

**Principal environmental variables that can interfere in the movement, survival and development of free-living larvae in the microclimate of a pasture**

Various factors that act simultaneously can favor or inhibit the movement of larvae in grass. When evaluated in isolation, temperature is one of the variables that becomes responsible, at certain ranges, for a number of behavioral alterations among larvae in the pasture. These include altered capacity to move, a reduction in survival period in the environment and accelerated development. Callinan & Westcott\(^\text{[6]}\), for example, showed that the highest rate of larval migration (Ostertagia spp. and *Trichostrongylus* spp.) can be observed on those days when the temperature remains around 13 °C. Another study by Williams & Bilkovichi\(^\text{[38]}\) reported that the ideal temperature range for the development and migration of larvae (*Ostertagia ostertagi* Stiles) is between 16.1 and 34.2 °C, while Silangwa & Todd\(^\text{[39]}\) affirmed that the optimal temperature for larval development (*Haemonchus* spp., *Cooperia* spp. and *Trichostrongylus* spp.) is around 26.6 °C. However, these observations contradict results from Barger et al.\(^\text{[40]}\), which showed low recovery of L3 (*Ostertagia* spp. and *Cooperia* spp.) in pastures when the temperatures were above 20 °C and below 13 °C. They also contrast with the study of Amaradasa et al.\(^\text{[41]}\), observing that temperatures around 23 to 31 °C do not interfere in the movement of larvae (*Haemonchus* spp.) in the environment and with that of Rogers\(^\text{[42]}\), where temperatures between 05 and 45 °C markedly favored the migration of larvae to grass (Table 1).

Even though there are still controversies over the migratory behavior of infective larvae in the pasture, it is clear that there is a tendency for random vertical and horizontal movement, which is only favored when the conditions of humidity and temperature are adequate\(^\text{[6]}\). More specifically, it can be said that an increase in the recovery rate of larvae is generally associated with a rise in these parameters.

When temperatures are favorable, luminosity of approximately 620 LUX\(^\text{[42]}\) can be a determining factor in the stimulation of larval migration in the pastures\(^\text{[43]}\), because solar radiation has the capacity to kill helminth eggs (*Haemonchus contortus* (Rudolphi) Cobb and *Trichostrongylus colubriformis* Giles) quickly, making larval development and migration inviable\(^\text{[44]}\). However, depending on the environmental conditions, such as temperature, humidity, precipitation and, especially for forage species, light, as well as wind, mist or evaporation, there may not be any relationship with the availability of L3 in pastures. The larval microhabitat, composed of the vegetation cover, may provide its own microclimate, and therefore larvae become subject to it\(^\text{[16]}\).

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Infective juvenile (genus)</th>
<th>Author</th>
<th>Year</th>
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<tbody>
<tr>
<td>05 to 45</td>
<td><em>Trichostrongylus</em> spp.,</td>
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<td></td>
<td><em>Haemonchus</em> spp.,</td>
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<td><em>Ostertagia</em> spp.,</td>
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<td><em>Chabertia</em> spp.</td>
<td>Rogers(^\text{[40]})</td>
<td>1940</td>
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<tr>
<td>16.1 to 34.2</td>
<td><em>Ostertagia</em> spp.</td>
<td>Williams and Bilkovich(^\text{[38]})</td>
<td>1973</td>
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<td>26.6</td>
<td><em>Haemonchus</em> spp.,</td>
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<td><em>Cooperia</em> spp.,</td>
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<td></td>
<td><em>Trichostrongylus</em> spp.</td>
<td>Silangwa and Todd(^\text{[39]})</td>
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<td>13 to 20</td>
<td><em>Ostertagia</em> spp.,</td>
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<td><em>Cooperia</em> spp.</td>
<td>Barger et al.(^\text{[40]})</td>
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<td>13</td>
<td><em>Ostertagia</em> spp.,</td>
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<td></td>
<td><em>Trichostrongylus</em> spp.</td>
<td>Callinan and Westcott(^\text{[6]})</td>
<td>1986</td>
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Generally, in conditions with high evaporation, lower recovery rates are presented by larvae in pastures\(^{[46]}\). The best conditions for larval development and migration appear when the humidity is above 43%\(^{[6, 38, 46]}\). Thus, just as higher temperatures (above 12.8 °C) stimulate infective larvae to migrate to grass, they also make it unviable for larvae to move because they increase the evaporation rate and, consequently, reduce the relative humidity in the pasture microclimate\(^{[47]}\). It should be noted that the simple presence of L3 in the pasture, however, does not necessarily mean they are available to be ingested by the susceptible hosts\(^{[47]}\), as most of the L3 can be found dead or may migrate from the fecal pat or forage, moving into the soil\(^{[46]}\).

In addition, various other factors can also have an indirect natural action on the reduction of the larval recovery rate and/or availability for animal consumption. In field conditions there can be the participation of microorganisms, which may have a preeminent influence on the degradation and mortality of L3 in recently deposited fecal masses\(^{[46, 49]}\), but coprophagous coleopterans can also participate\(^{[11]}\), increasing their activities in the wet season, breaking down fecal masses and interfering in L3 availability in the environment.

In the Brazilian Midwestern region, summer is the season when larval recovery is highest, due, principally, to the greater number of days with measurable rainfall, high relative humidity and higher temperature at soil level, with minimum and maximum being 19 and 42 °C, respectively\(^{[46, 50, 51]}\). These affirmations are borne out by results observed by Amaradasa et al.\(^{[41]}\) and Quadros et al.\(^{[52]}\), who observed that rainy periods provide appropriate conditions for the development of infective larvae in the pastures. Fakae & Chiejina\(^{[53]}\) confirm that the migration of larvae is greatest in the wet period, but they emphasize that environmental contamination can extend up to four weeks after the start of the dry season. Similar observations were made by Gronvold & Hogh-Schmidt\(^{[54]}\), after simulations of rain on fecal pats previously contaminated by infective larvae of *Ostertagia ostertagi*. These authors noted that this simulation resulted in low larval recovery, but when the fecal masses were previously wetted, the movement of larvae to the surface of the pat was triggered. Furthermore, they observed that 90% of infective larvae are passively transported by splashes and drips. Only 10% of larvae are capable of migrating actively in water film or are carried into soil by water droplets.

In extreme situations, such as at moments in which temperature and humidity are very high or very low, as well as in sparse or very heavy rains, this can jeopardize L3 development, or inhibit the migration of infective larvae to the pasture\(^{[22, 55, 56]}\). Torrential rains may eliminate a very large number of infective larvae of *H. contortus* or result in excessive humidity, preventing adequate aeration of the fecal pat and of the soil surface, which will thus negatively influence the development and migration of larvae in grass\(^{[47]}\). This, however, contradicts results obtained by Lima\(^{[56]}\), who observed peaks of L3 in pastures after periods of heavy rain and confirmed that weak, continuous or sparse rain does not interfere at the level of environmental contamination. Aumont et al.\(^{[48]}\) verified the absence of any clear link between climate data and the population dynamics of infective larvae in the pasture. However, they observed that five consecutive days of rain are enough to increase the L3 population in the environment. Interesting results were also obtained by Agyei\(^{[59]}\), with a high positive correlation between the level of infective larvae in the pasture and the precipitation rate, making it possible to predict the most challenging levels and periods for L3 in pasture.

The influence of rain on the quantity of infective larvae that are possibly recoverable in grass was also evaluated by Khadijah et al.\(^{[50]}\), who observed that the moment of precipitation in relation to when the fecal pat was deposited in the environment may also favor or hinder L3 migration in the pasture. According to these authors, precipitation immediately before or up to two days after dropping the fecal pat in the environment benefits the recovery of infective larvae in the pasture. Besides, according to Callinan & Westcott\(^{[49]}\), when the humidity is clearly seen in the pasture, at approximately 90%, the rate of vertical migration becomes optimal and provides ideal conditions to increase the hatching, development and survival rates of infective larvae in the field environment\(^{[54]}\). It also favors the rate of horizontal migration among L3, who may move from 15 to 90 cm away from the fecal pat\(^{[54]}\).

Williams & Mayhew\(^{[61]}\) affirm that the optimal mean monthly precipitation for larvae to abandon fecal masses is about 50 to 120 mm. This is corroborated by results from Heck et al.\(^{[49]}\), who showed that hydric supply of 50 mm/month is enough to allow infective larvae to survive in the pasture microclimate. It can be inferred, therefore, that the volume and regularity of precipitation that favor a rise in humidity are more important than the number of days with rain\(^{[56, 62]}\). Soil humidity supplies ideal conditions for the development and survival of helmint eggs within the recently deposited fecal masses and for the grasses that protect the fecal pat from solar rays and desiccation\(^{[59]}\). At times of the year in which desiccation of the fecal pat is less severe, the dew may be enough to allow larval migration (*H. contortus, T. colubriformis* and *Nematodirus battus* (Crofton and Thomas) in a more gradual manner. The soil and presumably the vegetation are secondary reserves of infective larvae in the environment\(^{[51]}\).
It can be noted that the variable humidity, arising from regular rains, has a direct influence on the recovery rate of larvae in the pasture. However, it is important to emphasize that the absence of rains does not prevent larvae from developing in the environment, as the humidity contained in the fecal masses is enough to permit optimum development until the infective stage (L3). Indeed, the confinement of L3 within fecal masses, recently deposited or not, confers protection against solar rays and thus reduces larval desiccation. The fecal pat is therefore an important reserve for infective larvae during droughts\cite{12, 46, 48, 62}. The accumulation of L3 within the fecal masses during this period may lead to mass migration of the larvae as soon as the rainy season starts, producing epidemiologically significant concentrations of infective larvae in pastures, even in the winter and spring of the next year, which makes the pasture a source of intense infection for livestock\cite{63}. It is therefore clear that cattle pastures do not become free of parasites (GINs) even after prolonged droughts\cite{60}. This knowledge supplies important support in establishing control strategies for environmental management and, consequently, control within the animal. Pasture rotation, for example, was long considered an efficient way to control gastrointestinal verminosis in cattle, but is today viewed with caution. It is known that the length of time that infective larvae remain in the field may vary from weeks to months in the wettest and driest periods of the year, respectively\cite{47}. Thus, the rotation scheme may be pointless, given that the fallow period may not be long enough to extinguish the infective stages that are available in the pasture environment.

In general, in any season, there is a consensus that an increase in the number of infective larvae in forage occurs only at certain times of day\cite{64}, usually during the coolest periods, always near sunrise and sunset\cite{55, 63}. However, studies reveal that larval migration in pastures can also occur at all times of the day and night\cite{66}, and even at midday\cite{71}.

Whatever the moment of greatest or lowest L3 density in the forage, it is certain that, as well as the aforementioned factors, there is a close relationship between the number of infective larvae recovered from the field and the presence of green matter\cite{55}. The proportion of dry matter (DM) available in the pasture is one of the most important variables to determine the risk of parasitic infection\cite{66}. According to Heck et al.\cite{54}, the presence of 3960 L3/Kg DM can be considered high-risk, since if susceptible cattle ingest up to 600 L3 per day this can reduce efficiency in the use of nutrients they ingest, and can lead to a fall of up to 50% in weight gain\cite{69}.

Normally, L3 reach higher portions of vegetation when the forage is higher, growing interlaced and with broad leaves\cite{57}. This statement is confirmed by Goldberg\cite{69}, who justified high larval density due to the greater retention of humidity in the pasture microclimate. In turn, Silangwa & Todd\cite{69} observed that the vertical migration of L3 is influenced not only by the height but also by the number of leaves and the surface properties of the plant. These properties can direct and determine larval migration speed, depending on the quantity of veins, resulting in the formation of narrower films of water, or smooth leaves, which favor the formation of broader migration pathways\cite{68}.

In experimental conditions, the quantity of larvae likely to be recovered is lower when the fecal pat, contaminated with helminth eggs, is deposited in forage of up to 5 cm in height, when compared to forage more than 30 cm high. This characteristic is probably due to solar radiation, which causes the destruction of many eggs and death of larvae in shorter forage\cite{67}. This is mainly due to desiccation, which is considered the most lethal of all microclimatic interferences\cite{69}. It can therefore be inferred that the recovery of larvae in the environment is significantly influenced by the height at which they are collected (stratum); the season, which affects the greater or lesser incidence of solar rays; and the interaction between the stratum and the season\cite{70}.

Generally, most of the L3 are found in the soil\cite{71}, which is also an important reserve for viable larvae during dry periods; these may also be found at the base of forage plants at a height of approximately 2 cm\cite{66}. Callinan & Westcott\cite{66} were more specific and reported that only about 20% of larvae are found in forage and around 80% in the soil and, therefore, the recovery of larval stages in soil can be eight times greater than in grass. These results contradict the observations of Lima\cite{134}, who stated that when microclimatic conditions were favorable, L3 vertical migration can occur with a greater presence of larvae in the upper region of grass (up to a height of 56 cm), demonstrating that GINs in cattle are capable of large vertical movements in forage plants.

It is observed that there are frequently broad variations in the number of L3 recovered from samples of forage\cite{111}. Even after feces have been deposited on the pasture with a known number of infective larvae, the number of larvae recovered is always a small fraction of the total number present in the sample deposited\cite{46}, which makes the density of recovered L3 always lower than expected. In general, only 1 to 3% of infective larvae are recovered from the pasture\cite{62, 57}, while up to 75.3% can be recovered from the soil\cite{32}, and there may be a high disparity between forage species\cite{15}. This is noted by Besier & Dunsmore\cite{44}, observing larval recovery rates of 0.03 and 0.007% after rainfall of 8 and 26 mm over four consecutive days and one day after the fecal mass was deposited on the soil, respectively.
The direction in which larvae move in the grass can also be affected by environmental factors, since in the absence of light, the larvae start to present migrations that are equally downwards and upwards, to the right and to the left, proving that these gradients direct and stimulate larval migration in the environment[6]. However, according to Callinan & Westcott[40], in the field, because the variables that affect the migration rate cannot be controlled, it is not possible to predict the behavioral responses of larvae in these situations.

**Influence of the forage species on the survival, movement and development of free-living stages of gastrointestinal nematodes**

The choice of a gramminaceous species for use in cattle pastures has to be made carefully, because this can significantly influence the population dynamics and vertical migration rate of ruminant infective larvae. As was observed by Amaradasa et al.[42], who noted a greater number of nematodes on forage grasses of the species *Paspalum notatum* (Fluegge) than of *Cynodon dactylon* (Linnaeus) Persoon; by Carneiro & Amarante[57], who showed that generally *Panicum maximum* (Jacq.) provides a larger number of recoverable larvae than *Brachiaria decumbens* (Stapf) Prain and *C. dactylon*; by Sauressig[72], who observed that the migration and survival of L3 were greater in grasses of the species *Andropogon gayanus* (Kunth), compared to *B. decumbens*; by Knapp-Lawitzke et al.[71] who observed that the greater the leguminous content in the pasture, the larger the number of infective larvae possibly found; and by Quadros et al.[52], who observed that the risk of infection is probably more intense in areas of pasture composed of *Cynodon plectostachyus* (K. Schum.), due to its habit of growing flat, making the pasture area lower, compared to *P. maximum* and *A. gayanus*.

In most of Brazil, the epidemiological conditions are favorable to parasite development, especially in the pasture microclimate, and they may be very variable over time. Therefore, periodically quantifying the immature forms concentrated in the pasture may be an alternative to determine the moment of highest or lowest rate of environmental contamination, associated with the increase or fall in the parasite burden in cattle. Thus, a more up-to-date scheme of strategic control can be implemented, applying antiparasitic treatments at the right times, reducing direct and indirect losses arising from parasitism.

New anatomical-physiological studies are still needed to determine the real relationship between the plant species and L3 movements[16], so that all the variables can be isolated, reducing the interference of external factors that may distort experimental results.

**Influence of the species of gastrointestinal nematode on the survival, movement and development of free-living stages in the pasture microclimate**

The larval recovery rate, which corresponds to the migration capacity of L3 in the pasture, is influenced not only by the above factors but also by nematode species[52]. Survival differs even under identical environmental conditions.

*Haemonchus* sp., which is an extremely pathogenic helminth and widely distributed in Brazil and worldwide, flourishes at lower temperatures[10] and is less sensitive to ultra-violet radiation, if compared to nematodes of the genera *Nematodirus* and *Teladorsagia*[44]. Its continuation in fecal masses, even during the dry season, which in Brazil is winter, is fundamental to guaranteeing its survival[57] over periods of many months[40]. In the soil, *H. contortus* and *Teladorsagia circumcincta* (Stadelmann) can survive for up to one or two months, respectively, under the same environmental conditions[52].

Within fecal masses, the maintenance of free-living phases also varies considerably among species of GINs. As Khadijah et al.[58] show, infective larvae of the genus *Trichostrongylus* can remain longer inside the fecal pat than the L3 of nematodes of the genus *Haemonchus*. In addition, high temperature and precipitation during the rainy season can reduce the recovery of *Haemonchus* spp. in the pasture, with the best environmental conditions for their larvae within feces and grass being temperatures of approximately 17 °C together with low precipitation[57]. Similar conditions are also observed for the genera *Cooperia*, *Oesophagostomum* and *Trichostrongylus*, which present optimal temperature ranges between 13 and 26 °C[61].

It is important to emphasize that, despite the slight differences observed between nematode species as regards their capacity to migrate within forage[40], the few morphological distinctions that exist between them can be enough to increase or reduce attrition on the plant surface and increase or reduce the migration rate. This is the case with the genus *Oesophagostomum*, which not only presents greater robustness than other nematodes of veterinary importance, but also has undulations on the cuticle that make movement difficult, especially on forage plants with hairy surfaces and natural twists[54].
CONCLUSIONS

The free-living behavior of GINs in cattle in the pasture microclimate is influenced by a complex network of variables that may interfere directly in their migration, survival and maintenance, thus influencing infection rates. The isolation of each environmental variable to determine its level of interference in larval behavior in field conditions is not yet an accessible practice. What is known already is that meso and (especially) microclimatic alterations, mainly temperature and humidity, are principally responsible for the greatest impact on larval behavior. The contribution of the forage species used is also notable, given its capacity to supply an environment that is favorable to maintaining free-living phases. So too is the species of GIN, given the specific intrinsic characteristics each one presents for survival in the environment, or inside fecal pats.

As a result, the management of each rural property plays a key role in the effectiveness of parasite control, because each farm or region has its own environmental characteristics, be they meso or microclimatic. Knowledge of these variables may be used as an important tool in correctly implementing control strategies that aim to employ anti-helminthic treatments intelligently and sustainably, reducing the risk of animal infection and increasing the number of parasites in refugia, especially given the current situation of parasitic resistance. However, new field studies are still needed to clarify the real contribution of each climate variable to larval behavior in the pasture and the impacts on raising the infection risk and the animal parasite burden.

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