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Faecal water content and egg survival of goat gastro-intestinal strongyles under dry tropical conditions in Guadeloupe

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Abstract. Faeces from naturally infected goats were deposited on a natural grassland during the dry season in Guadeloupe (French West Indies) at different times throughout the day. The grass was either 7 or 20–30 cm tall. After a period of between several hours and 7 days, the number of viable strongyle eggs and the faecal water content were measured. Faecal temperature was recorded continuously. Faecal temperature was >40°–45° C at midday and dehydration was rapid between 8 a.m. and 2 p.m. Egg mortality was greater on short than on tall grass and higher in morning than in evening deposits. Minimal faecal water content during the first 36 h explained the 74%, 55% and 38% mortality rate for eggs of *Oesophagostomum columbianum* (OC), *Haemonchus contortus* (HC) and *Trichostrongylus colubriformis* (TC), respectively. In all, 5%–22% of the eggs of the latter species remained viable in a state of anhydrobiosis after 7 days on the ground. A delay of only 2 days between goat departure and irrigation would be sufficient to ensure that >95% of *O. columbianum* and *H. contortus* eggs and 70% of *T. colubriformis* eggs are destroyed.

In the humid tropical climate of the West Indies, internal parasitism of goats is characterized by *Moniezia* spp. and, above all, by gastrointestinal strongyles. *Haemonchus contortus* (HC) is the dominant species that influences the year-round growth of kids (Gruner et al. 1984a). *Trichostrongylus colubriformis* (TC) is also present, sometimes in very abundant numbers (Gruner et al. 1984b). On pastures, rainfall governs the abundance of larval populations, with the dry season strongly affecting egg development in the flat, dry part of Guadeloupe (Aumont and Gruner 1989). Irrigation accentuates the adverse effect of parasites, enabling all of the eggs to develop within 7–9 days from faeces deposit, when, in the absence of irrigation, development of *T. colubriformis* eggs is delayed (Gruner et al. 1989).

The aim of this work was to study egg survival of gastrointestinal strongyles after faeces deposition under dry conditions to determine the kinetics of the death rate and to demonstrate the effect of the microclimatic factor(s) most closely correlated to it. One of the practical consequences of the results obtained would be to estimate the delay in irrigating a plot after the goats leave, as a function of mortality evolution.

Materials and methods

The experiment took place in the dry part of the island during March, when the dry season was well established. Faeces passed during the night by naturally infected goats onto a wire mesh surface above a concrete floor were collected. Species determination (Gruner et al. 1989) showed the presence of *H. contortus* (HC), *T. colubriformis* (TC) and *O. columbianum* (OC) eggs.

Egg viability

Freshly collected faeces were distributed in gauze bags, each containing 20 g faeces. The bags were then deposited on a natural *Dicanthium caricosum* grassland, recently rehydrated, with two grass heights: 20–30 cm (tall herbage) and 7 cm (low herbage).

In the first experiment, aimed at studying the short-term effects of faeces drying (36 h), deposits were made at the beginning (6.00 a.m.) and the end (6.00 p.m.) of the day. Five repetitions were carried out for each treatment (height of herbage × time of deposit) and time of collection. Seven control samples per time of deposit were cultured for 7 days at 24° ± 2° C and 60% water content to identify and count larvae. At different times after deposit on the ground, samples were collected, weighed, re-humidified at 60% water content, then cultured for 7 days. For the 6 p.m. deposit, samples were collected on the next day at 6 a.m., 10 a.m., 2 p.m., 6 p.m. and at 6 a.m. on the following day. For the 6 a.m. deposit, samples were collected at 10 a.m., 2 p.m. and 6 p.m. on the same day and at 6 a.m. and 6 p.m the next day. At 1 week after deposit, larvae were extracted from faeces, from nearby grass (16-cm diameter), and from the soil (2.5-cm depth, 16-cm diameter) under the faeces. For estimation of the number of viable eggs that did not hatch, collected faeces were cultured for 7 days.

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In the second experiment, aimed at studying the effects of faeces drying over a longer period (4 days), deposits were made at 11 a.m. and 2 p.m. on low herbage; samples (five repetitions each) were collected the next day and thereafter at 7 a.m. and were cultured for 7 days.

Bioclimatic measurements

In the first experiment, temperatures at 2.5-cm depth in the soil, in faeces and at 5 and 15 cm (tall herbage only) in the vegetation were read with a digital voltmeter on the two plots (heights of herbage, 7 and 20–30 cm) at 6, 8, 10 and 12 a.m. and 2, 4 and 6 p.m. during the 2 days following deposits, then at 6, 11 and 12 a.m. and 6 p.m. on the following days. Mean temperatures were estimated at each level with four series-mounted copper constantan thermocouples. Dry and wet bulb temperatures of two ventilated psychrometers placed 5 cm above the ground on each plot were also measured.

In the second experiment, only the faecal temperature was recorded, and hourly means were integrated over the whole experimental period. Soil water content was estimated every morning at 8.00 a.m. and faecal water content was determined for each sample collected. Global radiation and wind speed at 2 m above the ground were measured next to the plots. Other meteorological parameters were available from a station 6 km from the experimental plot.

Statistics

As the inspection of residuals showed no clear deviation from the normal law, the log-transformation of the data was unnecessary. Comparison of samples from the same deposit could be made on the absolute values of the number of larvae. Comparison of samples from different deposits had to be made with reference to the number of larvae in the respective controls.

Results

The microclimate is shown in Table 1 and Fig. 1. Rain fell only in the form of short night showers. Tall herbage intercepted more radiation than low herbage, thus protecting the faeces (highest values for faecal temperature were, respectively, 48.5° and 56.1° C). Faecal water content remained stable or increased during the night with dew and showers and decreased during the day, mainly between 8 a.m. and 2 p.m. The greatest drying effect was observed on the 1st day after deposit, mainly on low herbage, and was slightly greater for the 6 a.m. deposit. Almost total dehydration was obtained after 48 h without rainfall in experiment 2 (Fig. 3).

Faecal temperature was closely related to the mean global radiation of the previous hour. These two variables were correlated with determination coefficients $r^2 = 0.859$ on low herbage and $r^2 = 0.772$ on tall herbage ($n = 31$). Global radiation alone explained about 80% of the variability in faecal temperature, the relationship being all the better where the vegetal canopy was short. As other climatic parameters were not recorded hourly, it was not possible to appreciate their effect.

The relationship between faecal water content and climatic parameters is much more complex. Faecal desiccation was studied after rehumectation due to heavy rainfall on three deposits during 3 dry days (days D0, D1 and D2 of Fig. 3). Cumulate evaporation during a given time depends on cumulate values of climatic parameters, radiation, air temperature, dew point, wind speed, faecal temperature and faecal humidity (which

Table 1. Climatic conditions recorded in March during experiments 1 and 2, in Guadeloupe, French West Indies

	Experiment 1 (7 days)		Experiment 2 (4 days)
	Low-herbage plot	Tall-herbage plot	Low-herbage plot
Air temperature, maximal (° C)	27.6–28.6		28.5–29.1
Air temperature, minimal (° C)	19.4–22.4		21.0–21.9
Air relative humidity, maximal (%)	90 –93		
Air relative humidity, minimal (%)	60 –82		
Global radiation ($MJ^{-2} \times day^{-1}$)	19.0–25.5		19.2–23.6
Rainfall (mm/day)	3.3		1.9
Soil temperature (2.5-cm depth)	32 –35.4	31.5–34.6	–
Water content of superficial soil at 8 a.m.	20 –22.7	23.6–27.6	–
Herbage temperature, maximal (° C):			
at 5-cm height	38.1–41.1	39.5–48.9	–
at 15-cm height	–	35.2–41.9	–

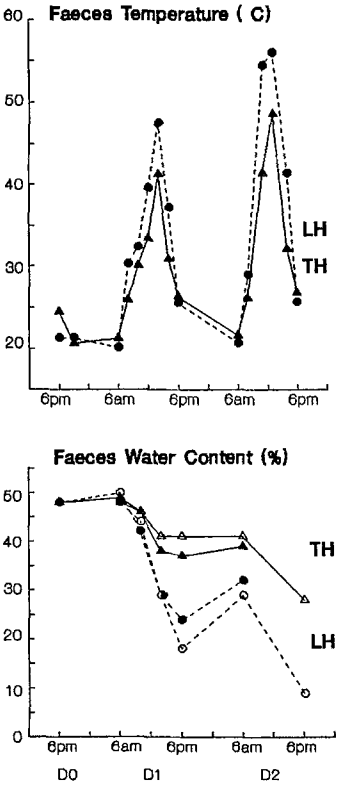

Fig. 1. Faecal temperature and water content during the first 2 days after deposit at 6 p.m. on low (●) and tall herbage (▲) and at 6 a.m. on low (*LH*) (○) and tall herbage (*TH*) (△) (experiment 1)

itself depends on cumulate evaporation). However, radiation, being the energy source, is the driving force of desiccation.

A problem arose during the night due to partial rehumectation by dew. As evaporation cumulated only during the daytime, this effect was discarded. However, the variation in faecal water content between evening and morning should normally introduce a disturbance into the relationship between evaporation and radiation. Fortunately, this was not observed in practice, the increased water content being moderate: 9.4% ± 2.1% on the 1st night (mean ± SD) and 11.4% ± 3.4% on the 2nd.

It can be shown that cumulate evaporation is related to water content as follows:

$$\int_0^t E\,dt = -mt(0) \times \frac{H(t) - H(0)}{1 - H(t)} + \Delta md,$$

where E(g/h) is instant evaporation, t(h) is time, H is water content (fraction of unity), the index t referring to time to and 0 representing the initial measurement after rainfall (day D0, 7.15 a.m.); mt(0) is the initial mass of wet deposit (mean ± SD, 26.1 ± 2.4 g), Δ md(g) is the cumulate mass of water brought by dew during the 2 successive nights (2.2 ± 0.1 g on the 1st night; 1.3 ± 0.4 g on the 2nd). In fact, as the sum was made only between the first and the last measurement of each day, it also took into account the residual evaporation of the beginning and, mainly, the end of the day.

A very good curvilinear relationship was found between cumulate evaporation, Y, and cumulate global radiation, X (MJ m^{-2}):

$$Y = 0.92 + 0.820\,X - 8.20 \times 10^{-3}\,X^2$$

$r = 9$ observations $\quad r^2 = 0.9889$.

Nevertheless, the best relationship was with time alone ($r^2 = 0.9968$); although statistical proof of the effect of radiation was not possible, its physical meaning is obvious. The study of instant values of evaporation did not give meaningful results because of the reduced number of measurements.

Viability of strongyle eggs

Table 2 gives the number of eggs deposited and their viability. The number of eggs deposited was greater in experiment 2, but their viability was lower. The percentage of the different species was the same in all deposits.

Table 2. Percentage of strongyle larvae obtained in the different control cultures

	Experiment 1		Experiment 2
	6 p.m. deposit	6 a.m. deposit	11 a.m. and 2 p.m. deposits
Eggs in faeces (*n*)	17400	16020	46800
Eggs that evolved into larvae	51.5%	79.4%	36.2%
H. contortus larvae	48.0%	46.0%	47.1%
T. colubriformis larvae	30.0%	36.0%	34.5%
O. columbianum larvae	22.0%	18.0%	18.4%

Effect of short-term treatments. All short-term (36-h) treatments displayed a significant egg death rate from the 1st day of collection (Table 3). Mortality was higher on low than on tall herbage and was greater for the 6 a.m. than for the 6 p.m. deposit on low herbage, the

Table 3. Effect of time and herbage height on the percentage of viable eggs (for 1000 eggs of control) in faeces

Time of collection (day – time)	6 p.m. deposit (day D0)		6 a.m. deposit (day D1)	
	Low herbage	Tall herbage	Low herbage	Tall herbage
D1 – 6 a.m.	468[a]	740[a]	–	–
D1 – 10 a.m.	185[a]	925[b]	897[b]	625[b]
D1 – 2 p.m.	255[a,b]	346[a]	120[b]	377[a]
D1 – 6 p.m.	379[a,b]	463[a]	150[b]	442[a]
D2 – 6 a.m.	212[a]	342[a]	97[b]	247[a]
D2 – 6 p.m.	–	–	121[a]	269[b]

[a,b] At any given time, different superscripts represent a significant ($P < 0.05$) difference between means

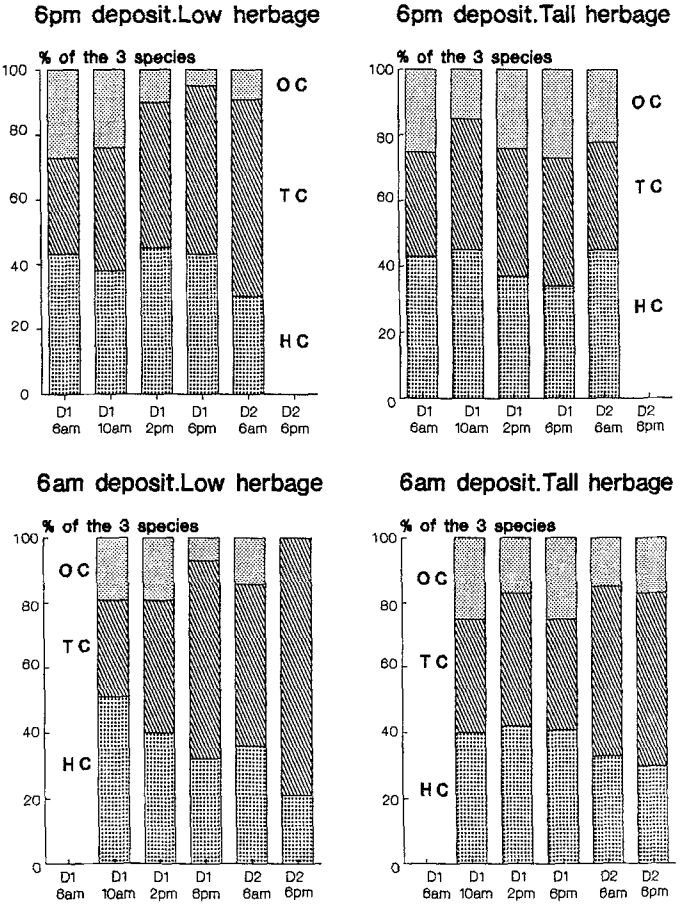

Fig. 2. Percentage of eggs of *H. contortus* (HC), *T. colubriformis* (*TC*) and *O. columbianum* (*OC*) among the surviving eggs from faeces during 36 h after deposit at 6 p.m. or 6 a.m. on low- or tall-herbage plots

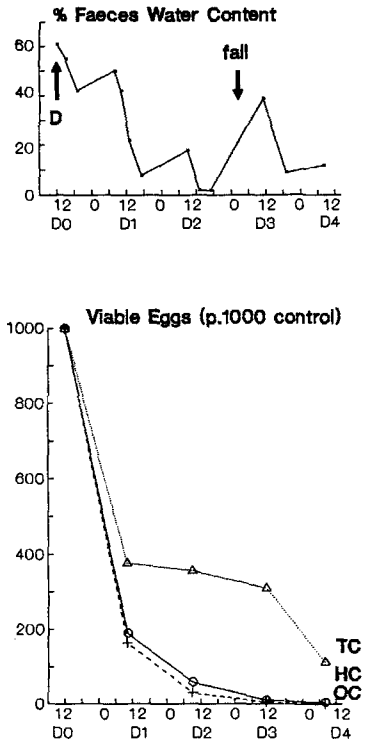

Fig. 3. Faecal water content and number of viable eggs remaining in the faeces during the 4 days following deposit on dry, low herbage for the species *H. contortus* (*HC*), *T. colubriformis* (*TC*) and *O. columbianum* (*OC*) (experiment 2)

results on tall herbage being similar. A comparison of the evolution of the ratio for the three species (Fig. 2) shows that the most extreme one (at 36 h) was observed when 6 a.m. deposits were made on short herbage. The OC percentage was reduced to almost zero, whereas the TC percentage was greatly increased. In contrast, for 6 p.m. deposits on tall herbage, the ratio observed for the controls was hardly affected. The two other cases (6 a.m. deposit on tall herbage and 6 p.m. deposit on short herbage) showed intermediate values.

Viability at 4 days after deposit. The results of 11 a.m. and 2 p.m. deposits (low herbage, experiment 2), showing little difference, were pooled (Fig. 3). As in experiment 1, the death rate of parasites was high beginning on day 1. The respective percentages of viable eggs of HC and OC dropped to 60‰ and 31‰ on day D2 and to 11‰ and 5‰ on day D3, respectively. TC eggs survived better, at 376‰, 357‰ and 310‰ on days D1, D2 and D3, respectively when faecal water content became lower than 1%. A shower on day D2 may have induced egg hatching and young larval mortality (only 113‰ of the viable elements remained on day D4).

Day 7 balance. After 7 days on the soil (experiment 1), the number of viable eggs in the faeces was significantly higher in the 6 p.m. deposit on tall herbage than in the three other treatments (Table 4). HC and OC had almost disappeared, whereas 5%–22% of viable TC eggs remained. Collection of faeces, soil and herbage enabled investigation for infesting larvae. The counts were corrected with extraction yields (Gruner et al. 1989).

Under dry conditions, OC almost disappeared; HC and TC larvae were found in soil and litter to a greater extent than in faeces or on herbage. Regardless of the number of viable eggs, the effects of grass height and time of deposit on the overall viable elements are not clear.

Relationship between egg survival and microclimate

On pasture, eggs were exposed to high temperatures that were sometimes >40°–45° C as well as to faeces drying. Although these two variables were not independent, for the same water content differences were not apparent between low and tall grass, which may demonstrate a thermal effect (Table 5). However, minimal faecal water content during deposit on the soil was closely related to the death rate (Fig. 4). The results of exponential as well as polynomial regressions between the death rate and minimal water content are presented in Fig. 4. Al-

Table 4. Number of viable eggs and larvae present in faeces, herbage and soil 7 days after faeces deposit (per 100 control larvae)

Species	Deposit	Viable eggs in faeces	Larvae			Total
			Faeces	Herbage	Soil	
H. contortus:	6 p.m., low herbage	0.09	0.05	0	22.36	22.5
	6 p.m., tall herbage	3.3	0.05	1.11	11.63	15.8
	6 a.m., low herbage	0.02	0.11	1.31	11.17	12.6
	6 a.m., tall herbage	0.02	0.26	0.98	7.23	8.7
T. colubriformis:	6 p.m., low herbage	6.8	0.16	0	3.92	10.9
	6 p.m., tall herbage	22.5	0.81	0.56	7.28	31.1
	6 a.m., low herbage	10.1	0.33	0.33	0.33	11.1
	6 a.m., tall herbage	5.2	0.38	1.32	1.64	8.5
O. columbianum:	6 p.m., low herbage	0.2	0	0	0.61	0.8
	6 p.m., tall herbage	0.2	0	0	0.61	0.8
	6 a.m., low herbage	0.1	0	0	0.52	0.6
	6 a.m., tall herbage	0	0.09	0	1.05	1.1

Table 5. Extreme ambient conditions in the faeces during the first 36 h on pasture and numbers of viable eggs (for 1000 control eggs of the species *H. contortus*, *T. colubriformis* and *O. columbianum*

Deposit	Sampling time	Time (h)		Min. faecal water content	Viable eggs for 1000 controls		
		40° C	45° C		HC	TC	OC
Deposits on short herbage:							
6 p.m., day D1	6 a.m.	0	0	48	420	463	580
	10 a.m.	0	0	40	147	232	205
	2 p.m.	2	1	29	241	387	108
	6 p.m.	3.5	1.5	23	345	676	91
day D2	6 a.m.	3.5	1.5	23	133	428	89
6 a.m., day D1	10 a.m.	0	0	44	1002	741	747
	2 p.m.	2	1	29	104	138	99
	6 p.m.	3.5	1.5	18	106	259	51
day D2	6 a.m.	3.5	1.5	18	75	136	59
	6 p.m.	9	5.5	9	56	265	3
Deposits on tall herbage:							
6 p.m., day D1	6 a.m.	0	0	48	662	798	834
	10 a.m.	0	0	47	894	933	1084
	2 p.m.	1	0	41	263	440	359
	6 p.m.	1	0	35	324	597	581
day D2	6 a.m.	1	0	35	321	372	349
6 a.m., day D1	10 a.m.	0	0	45	539	603	706
	2 p.m.	1	0	40	343	426	292
	6 p.m.	1	0	40	393	420	489
day D2	6 a.m.	1	0	40	177	360	159
	6 p.m.	4	1.5	28	177	393	205

though an exponential decrease would theoretically better describe this phenomenon, the observed normal distribution of the residual variability of the number of viable eggs (see Materials and methods) probably results in the polynomial adjustment being more realistic, as can be seen in Fig. 4 for the highest values for water content. For this reason, the determination coefficients for polynomial regression are retained, the respective values being 0.55, 0.38 and 0.74 for HC, TC and OC, with all adjustments being made at a probability level of at least $P<0.05$.

In Fig. 4, the effect of the time of deposit seems to be wholly compensated by the minimal faecal water content for HC and OC. For TC on low herbage at medium as well as low minimal water content, the effect of the time of deposit seems to remain, the dots for 6 p.m. and 6 a.m. deposits being, respectively, above and under the regression curve.

Discussion

This work demonstrates that eggs and larvae of *H. contortus*, *T. colubriformis* and *O. columbianum* are sensitive to the drying of their microenvironment under the climatic conditions of the West Indies. However, a thermal effect was not demonstrated, maybe because of the close relationship between faecal temperature and the drying rate. This drying factor impedes the development of larvae that are found in scarce numbers at 7 days after the deposits (Table 4) and induces considerable mortality, even in eggs (Table 3).

Herbage height and egg survival

From the data in Table 3, it seems that herbage height significantly reduces the death rate, at least for the 6 a.m. deposit, by protecting the faeces from solar radiation, thus attenuating the daily rise of temperature and the decrease in water content (Fig. 1). The species most affected by climatic stress is *O. columbianum*, the eggs of which totally disappeared in the 6 a.m. deposit after 7 days. Rose and Small (1980) observed large differences in the developmental capacities of a closely related species, *O. dentatum*, during the summer in Great Britain, depending on whether deposits were made in tall or low herbage. *H. contortus* is also greatly affected: it has long been known that sun-exposed faeces induce the fast death of eggs (Dinaburg 1944; Shorb 1943; Veglia 1915). Kauzal (1936) observed that short sequences of drying in the sun were lethal for *H. contortus* eggs as well as those of *Trichostrongylus* spp.

Time of deposit

The influence of the time of deposit seemed to be smaller than that of herbage height. In fact, the most important differences between herbage heights were observed on

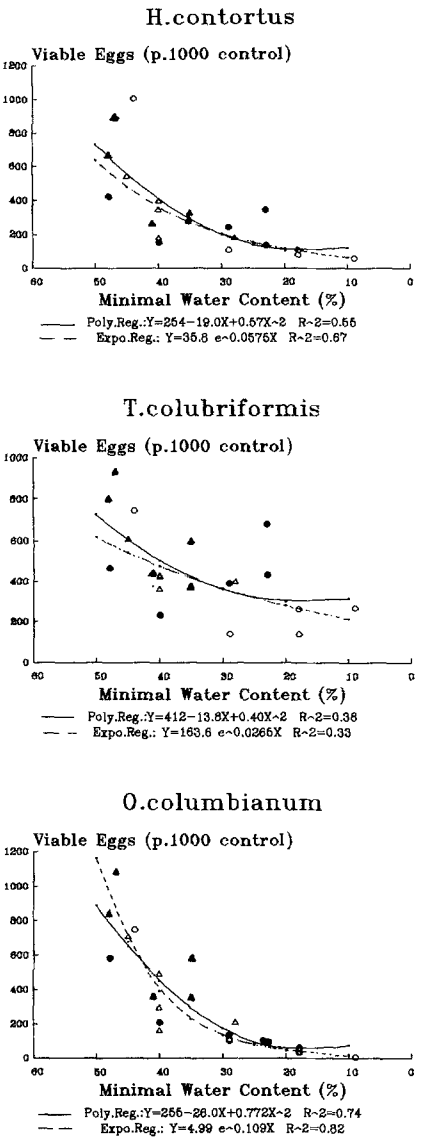

Fig. 4. Strongyle egg survival for between 4 and 36 h in caprine faeces deposited on the ground, as a function of minimal faecal water content during deposit (symbols as in Fig. 1)

the 6 a.m. deposits, which seemed more fragile than the 6 p.m. deposits (Table 3). However, this effect seemed to occur mainly in *T. colubriformis* (Fig. 4). Mauléon and Gruner (1984) observed the same phenomenon on various species in the Mediterranean climate.

Eggs deposited at 6 p.m. evolve during the night; thus, high temperatures and dehydration act on embryonated rather than non-embryonated eggs for the 6 a.m. deposit. Veglia (1915) observed that embryonated *H. contortus* eggs were more resistant to dryness than younger ones, and Mönnig (1930) found the same to be true for *Trichostrongylus* spp. but not for *H. contortus*. Under laboratory conditions, Silverman and Campbell (1959) observed good survival of developed *H. contortus* eggs in dehydrated faeces, but Rose (1963) did not confirm this under field conditions. The work of Waller and Donald (1970) and Todd et al. (1976) on eggs isolated from faeces confirm the sensitivity of *H. contortus* to desiccation and the better survival of eggs that are ready to hatch. For *T. colubriformis*, all authors confirm the improved resistance of embryonated eggs (Andersen and Levine 1968; Mönnig 1930; Waller and Donald 1970).

Egg survival and microclimate

During the day, faecal temperature was >40° C, once even reaching 50° C (experiment 1, low herbage, day 2; see Fig. 1). Veglia (1915) thought that some *H. contortus* eggs were still viable after 2 h exposure at 50° C but that they were all dead after 4 h. More precisely, Todd et al. (1976) estimated that 1% of non-embryonated eggs vs 4% of embryonated eggs survive a temperature of 45° C for 1 h. In *T. colubriformis*, Andersen et al. (1966) exposed faeces to different constant temperatures and observed that 84% and 4% of embryonated and non-embryonated eggs, respectively, survived at 40° C for 12 h. At 45° C, 2% remained after 12 h (embryonated eggs), and at 50° C, 1% were viable after 4 h (non-embryonated eggs). All embryonated eggs were dead after 8 h, and none of the non-embryonated eggs survived after 4 h (Agrawal 1966; Premvati and Lal 1961). With respect to the number of hours eggs were exposed to temperatures of >40° C, in our experiments (Table 5) lethal effects could be observed in the 6 a.m. deposits after 36 h on tall herbage (day D2, 6 p.m.) and in the three last collections on low herbage. However, such an effect was not obvious when significant correlations were obtained between the death rate and minimal faecal water content during deposits. This variable alone explains 55% and 74% of the respective variability in the number of viable eggs for *H. contortus* and *O. columbianum*. The results were more variable for *T. colubriformis* because of the ability of this species to survive in a state of anhydrobiosis. Waller and Donald (1972) showed for this species that whereas the death rate of non-embryonated eggs increased very sharply above 30° C, embryonated eggs could survive strong dehydration at high temperatures. Our observations support these results (Fig. 4).

In conclusion, during the dry season, faeces undergo heating and dehydration that is more rapid and intense when they are deposited on short herbage in the morning rather than in the evening. The minimal water content during the first 36 h seems to be the most pertinent variable, which alone explains 74%, 55% and 38% of the variability in the mortality of *O. columbianum*, *H. contortus* and *T. colubriformis* eggs, respectively. After 7 days on soil, only few larvae developed and remained in the soil and litter. In all, 5%–7% of *T. colubriformis* eggs remain viable in an anhydrobiotic state under the most stressful treatment. To wait only 2 days after the goats have left the pasture before undertaking irrigation would ensure the elimination of >95% of *H. contortus* and *O. columbianum* eggs and 70% of *T. colubriformis* eggs.

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References

Agrawal V (1966) The effect of temperature on the survival and development of the free-living stages of *Oesophagostomum columbianum* Curtice 1890. Trans Am Microsc Assoc 85:99–106

Andersen FL, Levine ND (1968) Effect of desiccation on survival of the free-living stages of *Trichostrongylus colubriformis*. J Parasitol 54:117–128

Andersen FL, Wang GT, Levine ND (1966) Effect of temperature on survival of the free-living stages of *Trichostrongylus colubriformis*. J Parasitol 52:713–721

Aumont G, Gruner L (1989) Population evolution of the free-living stage of goat gastro-intestinal nematodes on herbage under tropical conditions in Guadeloupe (FWI). Int J Parasitol 19:539–546

Dinaburg AG (1944) Development and survival under outdoor conditions of eggs and larvae of the common ruminant stomach worm, *Haemonchus contortus*. J Agric Res 69:421–433

Gruner L, Peroux F, Chemineau P (1984a) Distribution et rôle de l'haemonchose dans un élevage semi-intensif de chevreaux de race créole en Guadeloupe. In: Les maladies de la chèvre. Proceedings Int Coll, Niort, France, October 9–11. INRA, Paris, pp 705–715

Gruner L, Peroux F, Aumont G (1984b) Dynamique des population de parasites internes dans un élevage semi-intensif de chèvres créoles en Guadeloupe. In: Les maladies de la chèvre. Proceedings Int Coll, Niort, France, Octobre 9–11. INRA, Paris, pp 695–704

Gruner L, Berbigier P, Cortet J, Sauvé C (1989) Effect of irrigation on appearance and survival of infective larvae of goat gastro-intestinal nematodes in Guadeloupe (FWI). Int J Parasitol 19:409–415

Kauzal G (1936) Observations on the viability and resistance to desiccation of eggs and larvae of *Haemonchus contortus* and *Trichostrongylus* spp. Austr CSIRO Annu Rep 10:33

Mauléon H, Gruner L (1984) Influence de la déshydratation des fèces d'ovins sur l'évolution des stades libres de strongles gastro-intestinaux. Ann Rech Vét 15:519–528

Mönnig HO (1930) Studies on the bionomics of the free-living stages of *Trichostrongylus* spp. and other parasitic nematodes. Rep Dir Vet Serv Anim Ind Onderstepoort 16:175–198

Premvati G, Lal SS (1961) Effect of high temperature on the infective larvae of *Oesophagostomum columbianum* Curtice, 1890. J Parasitol 47:943–946

Rose JH (1963) Observations on the free-living stages of the stomach worm *Haemonchus contortus*. Parasitology 53:469–481

Rose JH, Small AJ (1980) Observations on the development and survival of the free-living stages of *Oesophagostomum dentatum* both in their natural environments out of doors and under controlled conditions in the laboratory. Parasitology 81:507–517

Shorb DA (1943) Survival on grass plots of eggs and pre-infective larvae of the common sheep stomach worm, *Haemonchus contortus*. J Parasitol 29:284–289

Silverman PH, Campbell JA (1959) Studies on parasitic worms of sheep in Scotland: 1. Embryonic and larval development of *Haemonchus contortus* at constant conditions. Parasitology 49:23–38

Todd KS, Levine ND, Boatman PA (1976) Effect of temperature on survival of free-living stages of *Haemonchus contortus*. Am J Vet Res 37:991–992

Veglia F (1915) The anatomy and life history of *Haemonchus contortus* (Rud.). Rep Dir Vet Serv Anim Ind Orderstepoort 3/4:347–500

Waller PJ, Donald AD (1970) The response to desiccation of eggs of *Trichostrongylus colubriformis* and *Haemonchus contortus* (Nematoda: Trichostrongylidae). Parasitology 61:195–204

Waller PJ, Donald AD (1972) Effects of changes in temperature and saturation deficit on the survival of eggs of *Trichostrongylus colubriformis* (Nematoda: Trichostrongylidae). Int J Parasitol 2:439–447