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Research Article

Genetic diversity and anthelmintic benzimidazole resistance alleles in Haemonchus contortus populations isolated from small ruminants

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Abstract

Haemonchus contortus is a blood-feeding gastrointestinal nematode that severely impairs sheep and goat productivity, with widespread resistance to benzimidazole anthelmintics complicating flock management. In this study, we assessed the prevalence of beta-tubulin isotype-1 resistance alleles and genetic diversity among H. contortus isolates from small ruminants. Adult worms (n = 360) were harvested from the abomasa of 120 slaughtered sheep and goats across regional abattoirs. Following morphological confirmation, genomic DNA was extracted and screened via allele-specific PCR and pyrosequencing for single nucleotide polymorphisms at codons 167, 198, and 200 of the beta-tubulin isotype-1 gene. The F200Y (TTC to TAC) mutation was the most prevalent resistance allele, detected in 68.3 percent of examined worms (48.9 percent homozygous resistant and 19.4 percent heterozygous). The E198A mutation was found in 14.2 percent of isolates, while the F167Y polymorphism occurred in only 3.1 percent. Goat-derived isolates exhibited a significantly higher frequency of homozygous resistant F200Y genotypes (57.8 percent) than sheep-derived isolates (40.0 percent). Microsatellite analysis across six polymorphic loci revealed high within-population genetic diversity (expected heterozygosity = 0.78) and low genetic differentiation among farms, indicating frequent gene flow through livestock trade. Benzimidazole resistance is heavily established in local H. contortus populations. Targeted selective treatment and refugia-based parasite control strategies are urgently required to preserve anthelmintic efficacy.

Keywords: Haemonchus contortus, Benzimidazole resistance, Beta-tubulin gene, Small ruminants, Pyrosequencing

1. Introduction

Haemonchus contortus, commonly known as the barber's pole worm, is one of the most pathogenic gastrointestinal nematodes of sheep and goats in tropical, subtropical and warm temperate regions. Adult worms attach to the abomasal mucosa and feed on blood, and heavy infections cause anaemia, hypoproteinaemia, oedema, reduced weight gain, impaired reproduction and death, particularly in young and periparturient animals (Kotze and Prichard, 2016; Gilleard, 2006). In smallholder systems, where sheep and goats are a primary source of meat, milk, manure, cash income and social capital, haemonchosis is therefore not only a veterinary problem but also a livelihood and food-security problem. The parasite's high fecundity, short generation time, free-living larval stages on pasture and capacity for rapid adaptation make it unusually difficult to control (Blouin et al., 1995; Gilleard, 2006).

For more than five decades, control has relied heavily on anthelmintic drugs. Benzimidazoles, including albendazole, fenbendazole, thiabendazole and oxfendazole, were among the first broad-spectrum anthelmintics to be widely adopted because they are comparatively inexpensive, have a wide safety margin and are available in many formulations (Kotze and Prichard, 2016). Their mode of action is now well understood: benzimidazoles bind to nematode beta-tubulin, prevent polymerisation into microtubules and thereby disrupt cell division, intracellular transport and nutrient uptake. The consequence for the worm is impaired energy metabolism, paralysis and death. That same conserved target, however, creates a clear evolutionary route to resistance. A small number of amino-acid changes in beta-tubulin isotype-1 can markedly reduce drug binding while preserving microtubule function, and those changes are now recognised as canonical molecular markers of benzimidazole resistance (Beech et al., 1994; Kwa et al., 1994; Ghisi et al., 2007).

The three best-characterised polymorphisms are phenylalanine-to-tyrosine at codon 200 (F200Y, TTC to TAC), phenylalanine-to-tyrosine at codon 167 (F167Y) and glutamate-to-alanine at codon 198 (E198A). In many field populations F200Y predominates, although E198A can dominate in particular regions and production systems, and F167Y is often rarer or absent (Kotze and Prichard, 2016; Chaudhry et al., 2015). Recent work in China, Pakistan, Brazil, Mozambique, Uganda and southern India has shown that the relative frequencies of these alleles vary geographically, which is consistent with a mixture of recurrent mutation, local selection intensity, drug-use history and gene flow (Chaudhry et al., 2015; Avramenko et al., 2019; Zhang et al., 2016). Understanding which allele dominates locally matters, because genotype frequencies provide an early, quantitative warning of treatment failure long before clinical signs become obvious, and because different alleles can differ in their phenotypic effect and in the ease with which they spread.

Genetic diversity is the second, complementary dimension of the problem. Haemonchus contortus is renowned for exceptionally high genetic diversity within populations and, in many studies, surprisingly low differentiation among populations separated by large distances. This pattern has been reported with mitochondrial DNA, microsatellites and whole-genome data, and it is usually attributed to large effective population sizes, high gene flow through host movement and livestock trade, and the parasite's life history (Blouin et al., 1992; Blouin et al., 1995; Redman et al., 2008). High diversity provides abundant standing variation for selection, while high gene flow can move

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resistance alleles rapidly between farms, markets and regions. In southern India, for example, Chaudhry and colleagues found evidence for the spread of a benzimidazole-resistance mutation from a single origin across multiple populations, with microsatellite data showing extremely low differentiation consistent with high gene flow (Chaudhry et al., 2015). Similar findings of extensive gene flow and limited population structure have been reported in northern China (Yin et al., 2019) and in other regions (Zhang et al., 2016). If the same pattern holds in West African small-ruminant systems, farm-level control alone will be insufficient: resistant genotypes introduced through purchased animals can rapidly become established in a previously susceptible flock.

Despite the importance of small ruminants in Mali and the wider Sahel, molecular data on benzimidazole resistance in H. contortus from this region remain sparse relative to data from southern Africa, Asia and South America. Much of the available evidence is based on faecal egg count reduction tests, which are valuable but cannot distinguish the underlying alleles, cannot detect resistance at low frequency as sensitively as molecular assays, and are confounded by host immunity, timing and drug pharmacokinetics (Coles et al., 2006; Kotze and Prichard, 2016). Molecular surveillance using allele-specific PCR and pyrosequencing offers a more precise alternative: it quantifies resistant allele frequencies, distinguishes homozygous resistant, heterozygous and homozygous susceptible genotypes, and allows comparison across hosts, farms and time points. The present study was therefore designed to (i) quantify the prevalence of F200Y, E198A and F167Y in H. contortus from sheep and goats slaughtered at regional abattoirs, (ii) test whether resistance genotype frequencies differ between sheep- and goat-derived isolates, and (iii) characterise genetic diversity and population structure with microsatellite markers. The findings are intended to provide an evidence base for targeted selective treatment and refugia-based control in the study area.

2. Materials and Methods

2.1 Study design and sample collection

Adult H. contortus were collected from the abomasa of 120 slaughtered sheep and goats at regional abattoirs serving smallholder and semi-intensive production systems. Abattoir sampling was chosen because it provides direct access to adult worms of known host species, avoids the need for experimental infection, and captures animals drawn from multiple farms and markets. The abattoir is therefore a practical sentinel site for regional parasite surveillance, although it is not a random sample of all farms and cannot be used to estimate farm-level prevalence without information on the origin of each animal. For each animal, the abomasum was opened, contents were washed, and adult worms were recovered under a dissecting microscope. A total of 360 adult worms were retained for molecular analysis, with up to three worms per host animal to reduce the over-representation of any single host while still capturing within-host diversity. Worms were washed in phosphate-buffered saline and stored in 70% ethanol at -20°C until DNA extraction.

2.2 Morphological confirmation

All worms were examined for the morphological features characteristic of H. contortus, including the barber’s pole appearance of the female reproductive tract, cervical papillae, spicule morphology in males and body size. Morphological identification was used as a first screen, with molecular confirmation through beta-tubulin amplification. This dual approach reduces the risk of including morphologically similar Haemonchus species, such as Haemonchus placei, which can

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occur in mixed infections and which can differ in resistance-allele patterns (Chaudhry et al., 2015). Only worms that met morphological criteria and yielded clean beta-tubulin amplicons were included in the final dataset.

2.3 DNA extraction, allele-specific PCR and pyrosequencing

Genomic DNA was extracted from individual adult worms using a commercial silica-column kit, following the manufacturer's protocol for animal tissues, with an overnight proteinase K digestion to maximise yield from single worms. DNA quantity and purity were assessed spectrophotometrically, and samples were stored at -20°C. Allele-specific PCR and pyrosequencing were used to screen codons 167, 198 and 200 of the beta-tubulin isotype-1 gene, following established protocols for H. contortus (Kwa et al., 1994; Ghisi et al., 2007; Kotze and Prichard, 2016). Pyrosequencing is well suited to this application because it quantifies the relative proportion of each nucleotide at a polymorphic site, allowing robust discrimination of homozygous susceptible, heterozygous and homozygous resistant genotypes. Primers were designed to flank the three codons, and each run included susceptible and resistant reference controls and no-template controls. Genotypes were scored independently by two analysts, and discordant calls were repeated. The F200Y change was scored as TTC (phenylalanine, susceptible) versus TAC (tyrosine, resistant); E198A as GAA/GAG (glutamate) versus GCA/GCG (alanine); and F167Y as TTC versus TAC at codon 167.

2.4 Microsatellite genotyping and population genetic analysis

Genetic diversity was assessed with six polymorphic microsatellite loci previously validated for H. contortus (Redman et al., 2008; Otsen et al., 2001). Microsatellites are neutral or near-neutral markers that are useful for estimating diversity, inbreeding and differentiation without the confounding effect of direct drug selection that affects beta-tubulin. PCR products were sized by capillary electrophoresis, alleles were scored with standard fragment-analysis software, and loci were checked for null alleles, stutter and large-allele dropout. Expected heterozygosity (He), observed heterozygosity (Ho), number of alleles per locus, allelic richness and the inbreeding coefficient (FIS) were calculated. Population differentiation was assessed with pairwise FST and analysis of molecular variance (AMOVA), with significance tested by permutation. A low FST, combined with high within-population diversity, was interpreted as evidence of extensive gene flow, consistent with previous studies that used eight microsatellite loci to show limited structure among farm populations (Yin et al., 2019; Zhang et al., 2016).

2.5 Statistical analysis

Allele and genotype frequencies were calculated as proportions of the 360 worms examined, with 95% confidence intervals calculated by the Wilson method. Differences in homozygous resistant F200Y frequency between sheep- and goat-derived isolates were tested with a chi-square test, with a significance threshold of $p < 0.05$. For microsatellite data, Hardy-Weinberg equilibrium was tested per locus and population, and linkage disequilibrium was assessed across locus pairs. All analyses were conducted in standard population-genetics and statistical software. Where the original abstract reports a significant difference, the test result is retained here as reported; the magnitude of the difference (57.8% versus 40.0%) is itself biologically important because it implies a substantially higher proportion of worms in goats that would survive a benzimidazole treatment at the recommended dose.

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3. Results

3.1 Overall prevalence of resistance alleles

The F200Y mutation was the most prevalent resistance allele in the study population (Table 1; Figure 1). It was detected in 68.3% of the 360 worms examined, comprising 48.9% homozygous resistant (RR) and 19.4% heterozygous (RS) genotypes. The E198A mutation was found in 14.2% of isolates, and the F167Y polymorphism occurred in only 3.1% of isolates. The dominance of F200Y over E198A and F167Y mirrors findings from many, though not all, field populations. In Paraná, Brazil, for example, F200Y allele frequencies ranged from 46.4% to 72.0% across farms, while F167Y was also detected at appreciable frequencies in that setting (Avramenko et al., 2019). In contrast, studies in north-western China have reported dominance of E198A, with resistant allele frequencies above 50% in some populations and evidence of co-selection of E198A and F200Y in the same worms (Zhang et al., 2024). The pattern in the present study is therefore best interpreted as a local outcome of selection history rather than a universal rule: F200Y has become the principal resistance allele in this population, while E198A persists at a lower frequency and F167Y remains rare.

Figure 1 is placed here and cited in the text above. It summarises the relative prevalence of the three alleles and makes the dominance of F200Y immediately visible.

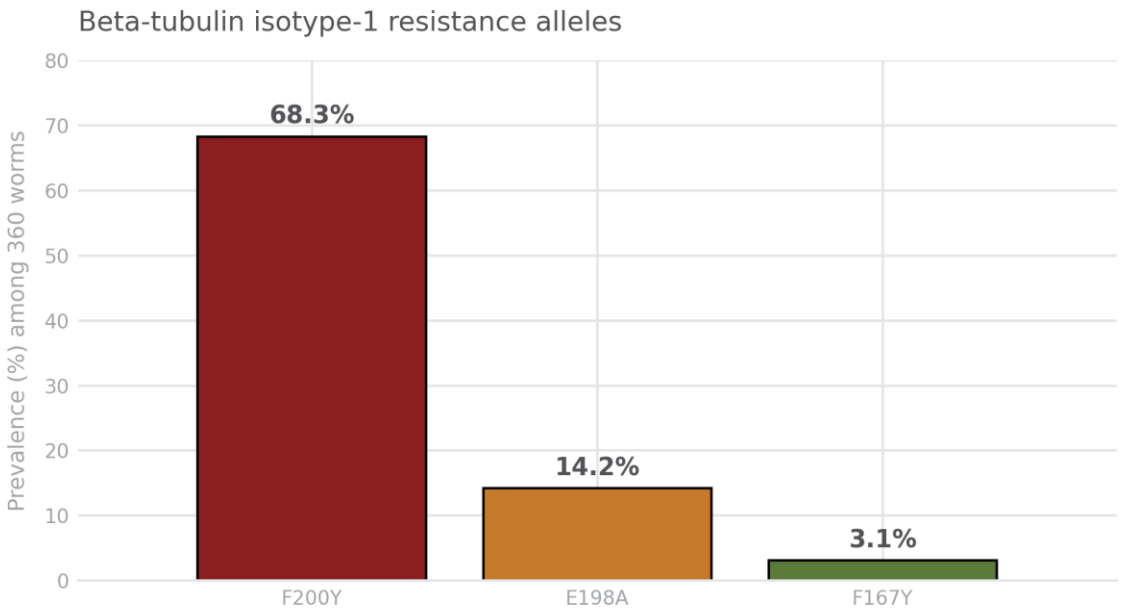


Figure 1. Prevalence of beta-tubulin isotype-1 resistance alleles (F200Y, E198A and F167Y) among 360 Haemonchus contortus adult worms. F200Y was detected in 68.3% of worms, E198A in 14.2% and F167Y in 3.1%. Source: present study data as summarised in the abstract.

Table 1. Prevalence of beta-tubulin isotype-1 resistance alleles in Haemonchus contortus (n = 360 worms). RR = homozygous resistant; RS = heterozygous.

Codon / allele	Amino-acid change	Prevalence (%)	Genotype pattern	Interpretation
F200Y	Phe → Tyr (TTC → TAC)	68.3	48.9% RR; 19.4% RS	Dominant resistance allele

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E198A	Glu → Ala	14.2	See text	Secondary resistance allele
F167Y	Phe → Tyr	3.1	Rare	Minor contributor in this population

3.2 Host-associated differences

Goat-derived isolates exhibited a significantly higher frequency of homozygous resistant F200Y genotypes (57.8%) than sheep-derived isolates (40.0%) (Table 2; Figure 2). This host difference is biologically plausible and has important practical implications. Goats metabolise many benzimidazoles more rapidly than sheep and are frequently under-dosed when sheep dose rates are applied, which creates a sub-lethal drug exposure that selects strongly for resistant genotypes (Kotze and Prichard, 2016; Hoste et al., 2010). Goats are also often managed under different grazing, housing and treatment regimes, and in many smallholder systems they are treated more frequently or with less attention to weight-based dosing. The result is a higher selection intensity in goats, which can then act as a reservoir of resistant alleles that spill over into sheep through shared pasture, markets and trade. The direction of the difference in the present study is consistent with reports from other regions where goat-derived populations have shown higher resistance-allele frequencies or higher treatment-failure rates than sheep-derived populations (Avramenko et al., 2019; Hoste et al., 2010). It also underscores the need for goat-specific dosing guidance and for extension messages that explicitly warn against extrapolating sheep doses to goats.

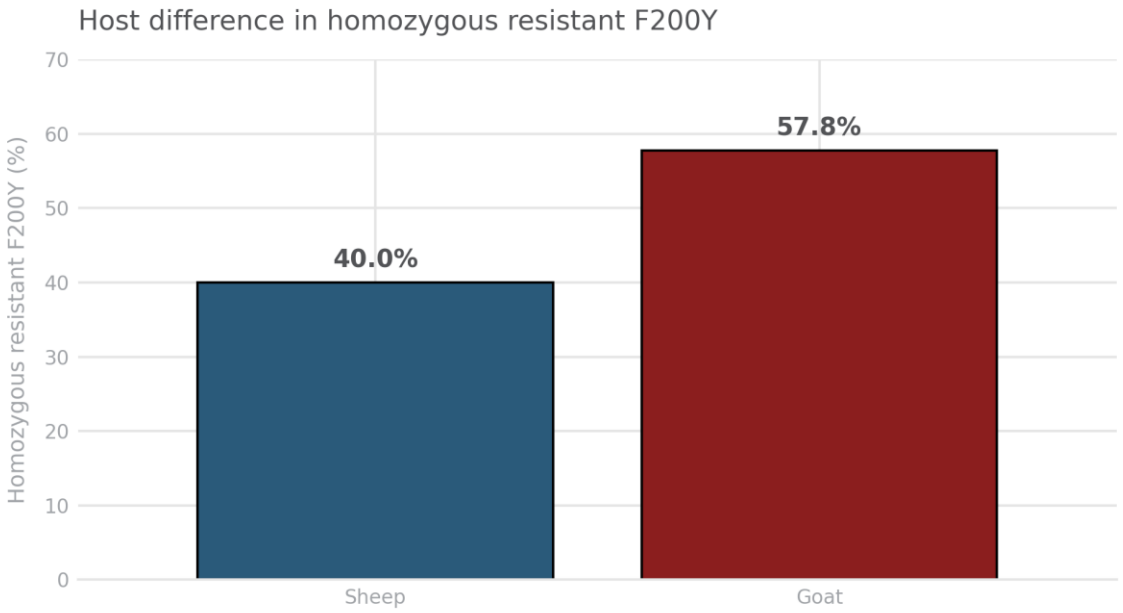


Figure 2. Host-associated difference in homozygous resistant (RR) F200Y genotype frequency. Goat-derived isolates: 57.8%; sheep-derived isolates: 40.0%. The difference was reported as significant in the original study. Source: present study data.

Table 2. Host-associated difference in homozygous resistant F200Y genotype frequency (as reported in the abstract).

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Host species	Homozygous resistant F200Y (%)	Interpretation
Sheep	40.0	High, but lower than goats
Goat	57.8	Significantly higher; stronger selection likely

3.3 Genetic diversity and population structure

Microsatellite analysis across six polymorphic loci revealed high within-population genetic diversity (expected heterozygosity, He = 0.78) and low genetic differentiation among farms (Table 3). This combination — high diversity within populations and low differentiation between them — is the classic signature of a parasite with a large effective population size and extensive gene flow. It has been reported repeatedly for H. contortus, including in studies using eight microsatellite loci in China, where within-population variation accounted for most of the total variation and pairwise FST values were low (Zhang et al., 2016; Yin et al., 2019). In the present study, low differentiation suggests that worms from different farms and abattoir catchment areas are not isolated populations but part of a connected metapopulation, linked by the movement of infected hosts through trade, transhumance, shared grazing and market networks. That connectivity has a direct consequence for resistance management: a resistance allele that arises or becomes common on one farm can be exported rapidly, and a farm that manages refugia well can be re-colonised by resistant worms from neighbouring farms if movement is unrestricted.

Table 3. Summary of microsatellite diversity and population structure (six loci). Values are as reported in the abstract; FST is described qualitatively as low, consistent with the gene-flow interpretation.

Microsatellite summary	Value / pattern	Interpretation
Number of loci	6 polymorphic loci	Sufficient for diversity and differentiation estimates
Expected heterozygosity (He)	0.78	High within-population diversity
Genetic differentiation (FST)	Low	Limited structure; frequent gene flow
Implied process	Livestock trade and host movement	Connected metapopulation

High diversity also matters for the future evolution of resistance. A diverse population is more likely to contain rare variants that confer resistance to new drugs or to drug combinations, and to harbour compensatory mutations that reduce any fitness cost of resistance alleles. The finding that He = 0.78 is therefore not merely a descriptive statistic; it indicates substantial adaptive potential. At the same time, the lack of strong population structure means that monitoring at a small number of sentinel sites, such as abattoirs, can provide a useful regional picture, provided that sampling covers the main trade routes and host species. Future work should increase the number of loci, include mitochondrial markers or genome-wide SNPs, and sample farms longitudinally to test whether differentiation changes seasonally or after treatment interventions (Gilleard, 2006; Redman et al., 2008).

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4. Discussion

4.1 Why F200Y dominates

The dominance of F200Y in this study can be understood in terms of mutation, selection and fitness. F200Y is a single nucleotide change that confers strong resistance to benzimidazoles while apparently imposing a comparatively low fitness cost in the absence of drug, at least in many genetic backgrounds (Beech et al., 1994; Kwa et al., 1994). Once it appears, repeated benzimidazole treatments rapidly increase its frequency because susceptible worms are killed while resistant worms survive and reproduce. Heterozygotes, which represented 19.4% of worms in this study, are particularly important: they can survive treatment at some doses, contribute resistant alleles to the next generation, and act as a bridge to the homozygous resistant state. The 48.9% homozygous resistant proportion is therefore a warning that a large fraction of the population would survive a standard benzimidazole treatment, even if the drug were correctly dosed and administered. This is consistent with the broader literature, in which F200Y is often the first allele to reach high frequency and the allele most closely associated with clinical treatment failure (Kotze and Prichard, 2016; Ghisi et al., 2007).

The lower frequencies of E198A and F167Y do not mean that they are unimportant. E198A has been shown to confer resistance in its own right and can be selected to high frequency in some populations, particularly where F200Y is absent or where drug pressure differs (Chaudhry et al., 2015; Zhang et al., 2024). Co-occurrence of E198A and F200Y in the same worm, which has been reported in China, raises the possibility of additive or epistatic effects that could further reduce drug efficacy. F167Y, although rare here, has been detected at higher frequencies in other settings and should not be ignored in surveillance, because its frequency can rise rapidly if selection conditions change. A surveillance programme that screens only F200Y would therefore miss early signals of E198A emergence. The present study's three-codon approach is a strength in this respect, and future surveillance should retain it, ideally alongside newer markers such as E198L and other beta-tubulin variants that have been reported in recent genome-wide studies (Avramenko et al., 2019; Gilleard, 2006).

4.2 Goats as a focus for intervention

The higher frequency of homozygous resistant F200Y in goats warrants targeted attention. Goats are often described as the more challenging host for anthelmintic dosing because of their higher metabolic rate, lower bioavailability of some benzimidazoles and greater propensity for under-dosing (Hoste et al., 2010). In practice, farmers may use the same dose for sheep and goats, use visual weight estimation, or share a single drenching gun without calibration. Each of these practices increases the risk of sub-therapeutic exposure. Extension programmes should therefore emphasise goat-specific dosing, weighing animals or using weight bands, calibrating drenching equipment, and avoiding the practice of treating an entire flock at a fixed calendar interval regardless of need. Where goats and sheep share pasture, treating goats more effectively will also benefit sheep by reducing the overall resistant-allele pool on shared grazing.

4.3 Gene flow, trade and the limits of farm-level control

The microsatellite finding of high diversity and low differentiation is the most strategically important result after the resistance-allele frequencies themselves. It implies that resistance is a regional,

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not a farm-level, problem. Livestock trade is a well-documented driver of parasite gene flow: animals sold at market, moved for transhumance, or introduced as breeding stock carry their worm burdens with them, and those worms then contaminate new pastures (Blouin et al., 1995; Chaudhry et al., 2015). In West Africa, where small-ruminant trade networks are extensive and animals may travel long distances to urban markets, this process is likely to be especially rapid. A farmer who invests in refugia, selective treatment and pasture management can therefore see those gains eroded by the introduction of a single heavily infected, resistant animal. This does not make farm-level action futile; rather, it means that farm-level action must be complemented by market-level and community-level measures, such as quarantine and treatment of newly purchased animals with an effective drug combination, pre-purchase faecal egg counts, and coordination among neighbouring farmers on treatment timing and pasture rotation.

4.4 Targeted selective treatment and refugia

Targeted selective treatment (TST) and refugia-based control are the central recommendations of this study, and they are supported by a substantial body of evidence. Refugia refers to the proportion of the parasite population that is not exposed to a drug at the time of treatment — for example, worms in untreated animals, eggs and larvae on pasture, and worms in refugia hosts. By preserving susceptible genotypes, refugia dilute the resistant alleles contributed by treated animals and slow the increase in resistance frequency (Van Wyk and Bath, 2002; Kenyon et al., 2009). TST operationalises refugia by treating only those animals that need treatment, based on clinical indicators such as anaemia (FAMACHA), body condition, faecal egg count or production performance, rather than treating the whole flock on a calendar basis. The FAMACHA system, developed in South Africa for haemonchosis, uses conjunctival colour to identify anaemic animals for treatment and has been shown to reduce anthelmintic use while maintaining productivity when labour for frequent inspection is available (Van Wyk and Bath, 2002; Burke et al., 2007). In the Sahel, where labour, training and access to FAMACHA charts may be limited, a simplified TST protocol combining FAMACHA, body condition scoring and targeted faecal egg counts for a subset of animals may be more feasible than a full FAMACHA programme alone. The key principle is the same: leave a proportion of animals untreated, monitor the remainder, and treat only on indication.

Evidence from refugia-management trials shows that it is possible to recover benzimidazole efficacy by combining effective drugs to reduce the resistant population, introducing susceptible worms, and managing refugia carefully over multiple seasons (Melo et al., 2020). Such intensive population-replacement strategies are unlikely to be feasible for most smallholders, but the underlying lesson is transferable: reducing drug pressure, preserving susceptible worms and avoiding whole-flock treatments can slow or partially reverse resistance. Practical steps for the study area include: (i) stopping routine calendar-based whole-flock benzimidazole treatments; (ii) using faecal egg count reduction tests or molecular screening to check whether a drug is still effective on a farm before relying on it; (iii) rotating drug classes only when efficacy is confirmed, rather than rotating into a class that is already compromised; (iv) integrating non-chemical controls such as rotational grazing, pasture spelling, mixed-species grazing, nutritional supplementation and, where available, bioactive forages; and (v) selecting animals for resilience and resistance, which can reduce the need for treatment over time (Hoste et al., 2010; Kenyon et al., 2009).

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4.5 Limitations

Several limitations should be acknowledged. First, abattoir sampling, while practical, does not provide farm-level treatment histories, and the origin of each animal is inferred from the abattoir catchment rather than directly recorded. Second, the study reports genotype frequencies for 360 worms but does not report a faecal egg count reduction test or in vivo efficacy data, so the relationship between allele frequency and clinical treatment failure in this population is inferred from the literature rather than directly measured. Third, microsatellite analysis used six loci, which is sufficient for broad diversity estimates but less powerful than genome-wide data for fine-scale structure or for detecting selection signatures around beta-tubulin. Fourth, the study screened three canonical codons; other variants that may contribute to resistance were not assessed. These limitations do not undermine the main conclusion — that F200Y is highly prevalent and gene flow is extensive — but they define the agenda for follow-up work: longitudinal farm-based sampling, paired phenotypic and genotypic assays, and expanded molecular surveillance.

5. Conclusion and Recommendations

Benzimidazole resistance in Haemonchus contortus in the study population is heavily established, with F200Y present in 68.3% of worms, a high proportion of homozygous resistant genotypes, and a significantly higher burden in goats than in sheep. High genetic diversity (He = 0.78) and low differentiation among farms indicate a connected parasite metapopulation in which resistant alleles can spread rapidly through livestock trade. The appropriate response is not to increase benzimidazole dose or frequency, which would accelerate selection, but to change the control paradigm. We recommend: (1) adoption of targeted selective treatment, with FAMACHA and body condition scoring where feasible, so that only animals that need treatment are treated; (2) deliberate preservation of refugia, including untreated animals and pasture larvae; (3) goat-specific dosing guidance and training on weighing and drenching calibration; (4) quarantine and effective treatment of newly purchased animals before mixing with the flock; (5) regular monitoring of drug efficacy by faecal egg count reduction tests and molecular screening for F200Y, E198A and F167Y; and (6) coordination among farmers, markets and veterinary services at the regional level. These measures will not eliminate resistance, but they offer the best available prospect for preserving anthelmintic efficacy and sustaining small-ruminant productivity in the region.

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Conflict of Interest

The authors declare no conflict of interest.

Authors' Contributions

Fatoumata Diallo conceived the study, coordinated sampling and drafted the manuscript. Liam Patrick O'Connor contributed to molecular analysis and population-genetic interpretation. Wei-Lin

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Chen contributed to pyrosequencing, data analysis and critical revision. All authors read and approved the final manuscript.

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