Biological control of ticks

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SUMMARY

Ticks have numerous natural enemies, but only a few species have been evaluated as tick biocontrol agents (BCAs). Some laboratory results suggest that several bacteria are pathogenic to ticks, but their mode of action and their potential value as biocontrol agents remain to be determined. The most promising entomopathogenic fungi appear to be *Metarhizium anisopliae* and *Beauveria bassiana*, strains of which are already commercially available for the control of some pests. Development of effective formulations is critical for tick management. Entomopathogenic nematodes that are pathogenic to ticks can potentially control ticks, but improved formulations and selection of novel nematode strains are needed. Parasitoid wasps of the genus *Ixodiphagus* do not typically control ticks under natural conditions, but inundative releases show potential value. Most predators of ticks are generalists, with a limited potential for tick management (one possible exception is oxpeckers in Africa). Biological control is likely to play a substantial role in future IPM programmes for ticks because of the diversity of taxa that show high potential as tick BCAs. Considerable research is required to select appropriate strains, develop them as BCAs, establish their effectiveness, and devise production strategies to bring them to practical use.

Key words: Biocontrol, entomopathogenic fungi, entomopathogenic nematodes, Ixodidae, parasitoids, predators.

INTRODUCTION

Since the beginning of the 20th century investigators have documented numerous potential tick biocontrol agents, including pathogens, parasitoids and predators of ticks (Jenkins, 1964; Mwangi, 1991; Mwangi *et al*. 1991*a*; Samish & Rahacek, 1999; Kaaya, 2003). Several authors have reviewed specific groups of natural enemies of ticks, including pathogens (Lipa, 1971; Hoogstraal, 1977; Chandler *et al*. 2000), nematodes (Samish, Alekseev & Glazer, 2000*a*, *b*; Samish & Glazer, 2001), parasitoids (Cole, 1965; Trjapitzin, 1985; Davis, 1986; Mwangi & Kaaya, 1997; Hu, Hyland & Oliver, 1998; Knipling & Steelman, 2000), and predators (Barre *et al*. 1991; Mwangi, Newson & Kaaya, 1991*b*; Kok & Petney, 1993; Samish & Alexseev, 2001).

In practice, ticks are controlled at present mostly by chemical acaricides (for detailed review see chapter by George, Pound & Davey in this Supplement). However, biological control is becoming an increasingly attractive approach to tick management because of: (1) increasing concerns about environmental safety and human health (e.g. the gradual increase in use of chemical insecticides in several countries is stimulating the growing market of 'organic' food); (2) the increasing cost of chemical control; and (3) the increasing resistance of ticks to pesticides. To date, biocontrol has been targeted largely at pests of plants, with only a few efforts to introduce biocontrol agents for the control of ticks. Nevertheless, the knowledge and experience accumulated in plant protection will aid in the development of tick biocontrol methods.

Classical biological control includes the recognition, evaluation and importation of a natural enemy from elsewhere, the conservation of local natural enemies and the augmentation of the biocontrol agents. Application methods can include individual inoculations or inundative releases of the natural enemies. Much effort has been applied to control pests by means of biological agents, often as part of integrated pest management (IPM) programmes (De Bach & Rosen, 1991; Van Driesche & Bellows, 1996). During the early 20th century efforts were made to import parasitoids into the USA for tick control (Larrousse, King & Wolbach, 1928; Cooley & Kohls, 1934; Alfeev, 1946). In addition, oxpeckers have been reintroduced into areas in Africa where these birds had become extinct (Davison, 1963; Grobler, 1976, 1979; Couto, 1994).

Ticks are obligatory blood sucking Arachnids that feed on vertebrates. While argasid ticks (soft ticks) feed for minutes or hours, the ixodid ticks (hard ticks) feed for days to weeks. In most cases, over 90% of the tick's life-cycle is spent off their hosts. Accordingly, two general strategies for controlling ticks

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with acaricides are in use – 'on-host' and 'off-host' control. On-host control strategies use the vertebrate as bait for ticks, relying upon the relatively high concentration of the pest on a small area, and kill ticks with a high potential to propagate. Further, this strategy can benefit from the often more stable environment of the host skin, e.g. temperature, relative humidity (RH) – factors especially important for biocontrol. However, off-host control strategies enable treatments far from the host, under conditions that in some cases are more suitable, e.g. high RH with little UV irradiation under trees. Off-host control can minimize exposure of individual vertebrate hosts to pesticides, but large areas of the environment may be exposed to such hazards. In both strategies, environmental hazards associated with tick control can be dramatically reduced if biocontrol techniques are efficiently applied.

In this review, we try to summarize and update published information on biocontrol agents that have the potential to suppress tick populations, emphasizing those not covered in a recent review of the subject (Samish & Rehacek, 1999).

PATHOGENS

The Bio Pesticide Manual (Copping, 2001) lists 96 commercial active ingredients based on microorganisms. Thirty-three are based on bacteria, 36 on fungi and eight on entomopathogenic nematodes. In contrast to the biopesticides used against off-host ticks and most plant pests, development of those targeted at ticks on hosts need to take into account the relatively high temperatures on the skin, the limited ability of the pathogen to penetrate via tick mouthparts while feeding, and, importantly, considerations of safety for people and animals.

Bacteria

Bacteria are commonly found in wild-caught ticks, but most of these bacteria are not considered pathogenic to the ticks (Noda, Munderloh & Kurtti, 1997; Samish *et al.* 1999*a*, *b*). Martin & Schmidtmann (1998) obtained 73 bacterial isolates from field-collected *Ixodes scapularis*, including 11 species of *Bacillus*, mostly in the *B. thuringiensis–B. cereus* species group. Tick haemolymph and cement plugs display bacteriocidal activity (Alekseev *et al.* 1995; Johns, Sonenshine & Hynes, 1998; Ceraul, Sonenshine & Hynes, 2002) that provide some protection against bacterial attack. Nevertheless, some bacteria show pathogenicity to ticks. For example, *Proteus mirabilis* is pathogenic to *Dermacentor andersoni* (Brown, Reichelderfer & Anderson, 1970). Bacteria also attack *Amblyomma hebraeum*, *Hyalomma marginatum* and *Rhipicephalus eversti eversti* (Hendry & Rechav, 1981) and apparently cause the Blackening disease of *Boophilus decoloratus*. Brum and colleagues (Brum, Faccini & Do Amaral, 1991*a*; Brum, Teixeira & Da Silva, 1991*b*; Brum & Teixeira, 1992) found the bacterium *Cedecea lapagei* (Enterobacteriaceae) to be pathogenic to *Boophilus microplus*; this bacterium infects ticks via the genital opening and under laboratory conditions can produce up to 100% mortality.

Tick – B. thuringiensis *interactions*. Since ticks ingest primarily host blood, it seems unlikely that *B. thuringiensis*, which attacks the midgut of insects, would successfully enter and cause mortality in ticks. However, Hassanain *et al.* (1997), performing Petri dish tests, found that three commercial varieties of *B. thuringiensis* (*B. t. kurstaki*, *B. t. israelensis* and *B. t. thuringiensis*) produced mortality when sprayed on unfed or engorged adults of *Argas persicus* or *Hyalomma dromedarii*. *B. t. kurstaki* was the most pathogenic (LC_{50} 215–439 μg/ml on day 5 PI for *Argas* and 1200–2344 μg/ml for *Hyalomma*). The susceptibility of the eggs of both tick species increased with increasing time after oviposition. Zhioua *et al.* (1999*a*, *b*) exposed *Ixodes scapularis* to *B. t. kurstaki* by dipping engorged larvae for 30 seconds in spore suspensions, and reported pathogenicity with an LC_{50} of 1×10^7 spores/ml.

The crystalline δ-endotoxin of *B. thuringiensis* is produced during sporulation and disrupts insect midgut walls (Gill, Cowles & Pietrantonio, 1992). Unlike spores, the δ-endotoxin shows specificity to particular insect taxa (Flexner & Belnavis, 2000), therefore it is unlikely that the δ-endotoxin kills ticks by causing toxaemia. Furthermore, the δ-endotoxin of *B. thuringiensis* subsp. *kurstaki* has to be activated by an alkaline pH and specific proteases. The extent to which the toxin will be activated in ticks with a midgut pH of 6·8 and intracellular cathepsins (pH optimum 3) (Sonenshine, 1991; Ramamoorthy & Scholl-Meeker, 2001) requires additional investigation.

Ticks ingest host body fluids through their mouthparts, but they also ingest water vapour, through both mouthparts and cuticle for hydration (Knulle & Rudolph, 1982). One mechanism involves a highly hygroscopic fluid secreted by the tick that is hydrated by water vapour from the surrounding atmosphere, and is then re-ingested into the tick. Therefore, it is plausible that spraying or dipping ticks in highly concentrated bacterial solutions could result in tick mortality if sufficient fluid was ingested to elicit pathogenic effects on the midgut. However, other mechanisms of pathogenicity are also plausible, including: the actions of other toxins such as *B. thuringiensis* exotoxins (Sebesta *et al.* 1981); negative effects associated with bacterial invasion of the haemocoel (Dubois & Dean, 1995); and the physical blocking of spiracles or other openings by bacterial spores.

B. thuringiensis products have proved to be the most popular biocontrol agents in agriculture

(Navon, 2000). However, because of the specific biology of ticks and the little information available, further research is required to elucidate the mechanism of bacterial pathogenicity to ticks. The mode of pathogenicity influences potential efficacy, as well as the design of delivery systems of bacterial pathogens for tick control.

Fungi

Over 700 species of entomopathogenic fungi have been reported, but only 10 species have been or are currently being developed for the control of insects (Hajek & St. Leger, 1994; Butt, Jackson & Magan, 2001). The most promising fungi are from the class Deuteromycetes (mitosporic fungi). The ability of entomopathogenic fungi to penetrate the cuticle of arthropods, the ability of a strain to kill several stages of the same pest and the relatively specific virulence of a single strain to one or a small group of pests make them good candidates as biocontrol agents. However, fungi also have some disadvantages: they are slow in killing their host, they need high humidity to germinate and sporulate, they are susceptible to UV irradiation, and some strains can potentially affect non-target arthropods (Ginsberg *et al*. 2002). Mass production can be quite costly, and the limited shelf-life of some products make them even more expensive. Many of these constraints can be addressed by advanced formulations. Most producers of fungal-based products suggest application methods similar to those used for chemical pesticides (Shelton & Roush, 2000).

Prevalence of tick–fungus interaction. In nature, 20 species of fungi have been reported to be associated with ticks. Some 13 species of ticks from 7 genera were found to be infected by fungi (Kolomyetz, 1950; Samsinakova, 1957; Steinhaus & Marsh, 1962; Cherepanova, 1964; Krylov, 1972; Samsinakova *et al*. 1974; Estrada-Pena, Gonzales & Casasolas, 1990; Mwangi, Kaaya & Essumen, 1995; Zhioua *et al*. 1999*a*; Guerra *et al*. 2001). Ticks collected in North East USA were infected primarily with *Verticillium* spp. and *Beauveria bassiana*; 10 species were isolated in Europe and 3 in Africa (Cherepanova, 1964; Samsinakova *et al*. 1974; Mwangi *et al*. 1995; Kalsbeek, Frandsen & Steenberg, 1995; Zhioua *et al*. 1999*a*). Of the engorged female *B. microplus* ticks collected from soil in Brazil, 24·5% were contaminated with *B. bassiana*, 10% with *M. anisopliae* (Da Costa *et al*. 2001), and 22% of the *R. sanguineus* nymphs were contaminated with fungi from 5 genera (Guerra *et al*. 2001). The percentage of ticks infected by fungi in collections from natural areas varies considerably, largely according to the stage and species of tick and to the ecological conditions at the sample sites. For instance, 7·5% of the adult *Ixodes ricinus* collected in central Europe during winter time were infected by fungi, compared to over 50% of ticks collected during the summer (Samsinakova *et al*. 1974). In northern Europe, between 6 and 32% of engorged *I. ricinus* females were infected by fungi in nature, depending on the season (Kalsbeek *et al*. 1995). Only 1·7% of the engorged *Rhipicephalus appendiculatus* females collected in Kenya died from fungal infection (Mwangi *et al*. 1995), and in the northeastern USA 4·3% of the collected unfed female *I. scaplularis* were infected (Zhioua *et al*. 1999*a*). In nature, a higher percentage of adult ticks seems to be infected by fungi than their pre-imaginal stages and engorged females seem to be most readily infected (Kalsbeek *et al*. 1995; Zhioua *et al*. 1999*a*).

Laboratory assays. When various fungal genera, species and strains were tested under optimal laboratory conditions, *M. anisopliae* and *B. bassiana* exhibited the strongest anti-tick pathogenicity (Guangfu, 1984; Gindin *et al*. 2001; Samish *et al*. 2001). In most cases, *M. anisopliae* strains were more virulent than those of *B. bassiana* (Mwangi *et al*. 1995; Castineiras *et al*. 1987; Barci, 1997; Kaaya & Hassan, 2000; Sewify & Habib, 2001; Zangi, 2003). Under laboratory conditions, at least 15 ixodid tick species and two argasid ticks were found susceptible to fungi (Samish *et al*. unpublished observation). Studies comparing the susceptibility of unfed larvae of *Boophilus annulatus*, *Hyalomma excavatum* and *R. sanguineus* to 12 fungal strains (from five species of fungi) gave the general impression that *Boophilus* and *Hyalomma* larvae showed similar susceptibility while *Rhipicephalus* larvae were more resistant. In contrast, engorged *H. excavatum* females were far more resistant to entomopathogenic fungi than females of the other two tick species (Gindin *et al*. 2003). Tick eggs, in contrast to many insect eggs, are highly susceptible to fungi and up to 100% of the eggs exposed to fungi under laboratory conditions did not hatch (Boichev & Rizvanov, 1960; Gorshkova, 1966; Castineiras *et al*. 1987; Monteiro *et al*. 1998*a*, *b*; Bittencourt, Massard & Lima, 1994*a*; Kaaya, 2000; Paiao, Monteiro & Kronka, 2001; Gindin *et al*. 2003). Fungal infection of engorged female ticks often resulted in longer periods of pre-oviposition, oviposition time, egg-incubation, and egg-hatching of the egg mass, as well as in lowered egg production (Gorshkova, 1966; Bittencourt, Massard & Lima, 1994*b*; Barci, 1997; Gindin *et al*. 2001). This suggests that there is a relatively long-lasting sub-lethal influence of the fungi on their tick hosts.

Comparison between the susceptibility of the unfed stages of *R. appendiculatus* and *Amblyomma variegatum* or of *H. excavatum* and *R. sanguineus* demonstrated decreasing susceptibility to fungi in progression through the larval, nymph and adult stages (Kaaya, 2000; Samish *et al*. 2001; Gindin *et al*. 2003), but unfed *I. scapularis* larvae were less susceptible than unfed adults (Zhioua *et al*. 1997).

Unfed larvae and nymphs seem to become more resistant to *M. anisopliae* after engorgement (Reis *et al.* 2001; Gindin *et al.* 2003).

Fungi take several days to kill ticks. For instance, the LT_{50} of *M. anisopliae* (at 1×10^7 spores/ml) for eggs, unfed larvae and engorged females of *B. annulatus*, *H. excavatum* and *R. sanguineus* generally ranged from <3 to 6.5 days; in some cases it extended to weeks. Engorged larvae of *H. excavatum* and *R. sanguineus* took twice as long to die than unfed larvae of the same species, and it took over 3 weeks for 50% of unfed adults to be killed by these fungi (Gindin *et al.* unpublished observation).

Field trials – off host. A 0·3 ha *Abies procera* plantation in Denmark was sprayed with *M. anisopliae* (BIPESCO strain) spores ($4–10 \times 10^{10}$ spores/m^2). Of the 67 unfed *Ixodes ricinus* ticks collected 2 weeks after treatment, 57% were contaminated with *M. anisopliae* (Nielsen *et al.* personal communication). Initial field trials used a commercial anti-termite mycoside based on *M. anisopliae* (ESC-1 strain, Bio-Blast Biological Termicide) against questing *I. scapularis* adults (spraying $4–6 \times 10^{10}$ spores/m^2). Within 4 weeks, 53% of the adults were killed (Benjamin, Zhioua & Ostfeld, 2002). When potted grass with adult or nymphal *R. appendiculatus* was sprayed with spores (1×10^9 spores/ml in water) and kept in the field, the mortality of ticks sprayed with *B. bassiana* was 96 and 36% for nymphs and adults, respectively; if sprayed with *M. anisopliae* the mortality reached 76 and 64% for nymphs and adults, respectively. The two fungal species together killed over 99% of the larvae. Similar results were obtained with *Amblyomma variegatum* (Kaaya & Mwangi, 1995; Kaaya, Mwangi & Ouna, 1996).

In Kenya, 5 acre paddocks were seeded with *R. appendiculatus* larvae and sprayed once a month with *M. anisopliae* or *B. bassiana* spores in an aqueous solution ($1·2 \times 10^9$ spores/m^2). During the rainy season the fungi had no effect upon the abundance of the ticks on cattle kept in the paddocks, but during the 3 months after the end of the rainy season *B. bassiana* and *M. anisopliae* reduced the tick population by 80 and 92%, respectively, compared with the control (Kaaya, 2000; Kaaya, Samish & Glazer, 2000).

Sack-cloth covering poultry houses that were heavily infested with the soft tick *Argas persicus* was sprayed with an *M. anisopliae* spore suspension (5×10^7 spores/ml in water with Tween 80 and 4% oil) and covered with a plastic sheet to maintain high humidity. The tick population was reduced by 53% within a week and after 3 weeks no live ticks could be found (Sewify & Habib, 2001). When two commercial *B. bassiana* mycoinsecticides (registered for use against pests of ornamentals and turf) were tested against *I. scapularis* nymphs in a residential area, the tick population was reduced by 59–89%, and some 80–90% of the recovered nymphs developed mycoses (Stafford & Kitron, 2002). Ticks inoculated with *B. bassiana* were released in a natural *D. variabilis* microhabitat from which live ticks were collected one year later. Fungal growth was observed after incubation of the ticks under laboratory conditions (Lucas, Fielden & Hererra, unpublished observations). Spraying of a paddock containing *B. microplus* larvae with *M. anisopliae* spores resulted in fewer larvae one week after treatment compared to the untreated paddock (Bittencourt, 2000).

Field trials – on host. Spraying *M. anisopliae* (1×10^8 spores/ml in water with Triton X-100) on gerbils one day after they had been infested with *R. sanguineus* nymphs reduced the number of engorged nymphs dropping off by 73% (unpublished observation). Spraying *M. anisopliae* spores (1×10^8 to 1×10^9 spores/ml in water) on cattle infested with *B. microplus* or *B. decoloratus* ticks at various development stages generally caused insignificant or low reductions (up to 50%) of the on-host tick population. However, up to 79% of the females collected from the sprayed cattle died in the laboratory, and their egg mass weight was reduced by up to nearly 50% (Castro *et al.* 1997; Correia *et al.* 1998; Bittencourt *et al.* 1999; Kaaya & Hassan, 2000). When *B. microplus*-infested cattle was treated one or four times with *Verticillium lecanii* ($3·5 \times 10^7$/ml, 5 l per head), the number of ticks was reduced by 48–79% or 94–99%, respectively (Camacho *et al.* 1998). In other trials, adult *R. appendiculatus* ticks were allowed to feed in ear bags on rabbits or cattle and were sprayed with *M. anisopliae* spores at dosages of $2·5 \times 10^8$ or 1×10^{10} spores per ear, respectively; 30% of the ticks on rabbits and 83% of those on cattle died. In addition, of the eggs laid by the *Beauveria*-treated females, none of those on the rabbits and only 48% of those on cattle hatched (Kaaya *et al.* 1996). Application of a gel formulation containing *B. bassiana* spores to the ears of horses reduced *Anocentor nitens* tick populations by 50% (Bittencourt *et al.* unpublished observation). When *B. bassiana* and *M. anisopliae* spores in water with Triton X-100 were sprayed on thoroughly washed ears of cattle, live *B. bassiana* spores were recovered up to 1 week and those of *M. anisopliae* up to 3 weeks after application (Kaaya *et al.* 1996). However, fungal spores suspended in water and sprayed on cattle were found to be virulent to *Boophilus* ticks for less than a week (Castro *et al.* 1997; Bittencourt *et al.* 1999), and most deaths of feeding *R. appendiculatus* occurred 5–10 days after fungal infection (Kaaya *et al.* 1996).

In several experiments live ticks were collected from a fungus-infested field or from their vertebrate hosts and incubated under optimal laboratory conditions. A high percentage of these ticks died and fungi grew on many of them even though low tick mortality was observed in the field or on hosts in the

same experiments. This suggests that under natural conditions the conidia often adhere to the tick integument, at least for a short time, but in many cases they do not germinate or penetrate the cuticle, and/or cause only a sub-lethal infection under field conditions.

Formulation. In most laboratory tests the spores were suspended only in water with a small amount of dispersing agent. Kaaya & Hassan (2000) compared the anti-tick effect of a suspension of *M. anisopliae* spores in water with 1% Tween-80 with or without 15% peanut oil. Unfed nymphal and adult ticks were immersed in the suspension and then kept outdoors on vegetation. The mortality of *A. variegatum* treated with the oil suspension was 30% higher for nymphs and 2·7 times higher for adults, and for *R. appendiculatus* 15% higher for nymphs and 4·3 times higher for adults than in applications with the water carrier without oil. The influence of the oil itself on the ticks has still to be clarified. In another trial, a powder formulation was prepared by mixing 1 volume of *M. anisopliae* spores with 9 volumes of various powders and was tested against *R. appendiculatus* adults feeding on cattle in ear-bags. The spore mixture with millet powder caused 100% mortality, maize 79%, sorghum 64% and starch 53% (Kaaya & Hassan, 2000). Treating *A. nitens*-infested ears of horses with a *B. bassiana* suspension in water resulted in less than 20% tick mortality, while their application in a polymerized pulp gel resulted in more than 50% mortality (Bittencourt *et al*. unpublished observation).

Clearly, the formulation in which the spores are applied is crucial to the level of control obtained with fungus-based anti-tick compounds, but very little has been published as yet on the subject. Much information in formulating fungi for use against free-living ticks can be obtained from experiments on fungal spores for the control of insect pests, but considerable research is still required to develop satisfactory formulations for the control of ticks while they are feeding on vertebrate hosts. Finally, additional research is needed to find more virulent and specific fungal strains.

Entomopathogenic nematodes

Entomopathogenic nematodes (EPNs) of the families Heterorhabditidae and Steinernematidae are known to be obligatory parasites of insects. The only free-living stage of the nematode, the third/infective juvenile (IJ), actively locates and enters the host via natural openings, and then releases symbiotic bacteria that kill the host insect within 24–72 h. The nematodes then multiply within the host cadaver and 6–18 days post infection thousands of IJs are released into the environment. The most common natural habitat of these nematodes is moist ground. The IJs are well adapted to the changing conditions of moisture, temperature, texture and chemical composition associated with different soil types (Glazer, 2001).

The EPNs are known to be pathogenic to over 3000 insect species, whereas each strain may often be relatively specific to a small group of hosts and thus their effects on most beneficial insects have been found to be negligible (Poinar, 1973; Gaugler, 2002). They are produced commercially on four continents, mainly in cottage industries, but also in large fermenters (up to 80 000 l), for the control of insect pests of forests and agriculture (Georgis & Manweiler, 1994). About US$10 million-worth of nematodes for the control of insects were sold in 1998; they were used either as an additive to irrigation systems or as sprays from the ground or air.

Tick–nematode interactions. EPNs penetrate engorged female *B. annulatus* ticks almost solely via the anus or genital pore (unpublished observations). Heterorhabditid nematodes killed engorged *B. annulatus* females in Petri dishes after less than 2.5 h of exposure, whereas steinernematid nematodes needed more than 4 h to penetrate into ticks (Glazer Alekseev & Samish, 2001). The injection of a single heterorhabditid nematode into a tick can cause mortality (Glazer *et al*. 2001). The dosages of EPNs needed to kill 50 or 90% of ticks are comparable to that used commercially in the control of insect pests of plants, but the time required to kill ticks is often relatively long (Table 1).

Tick mortality caused by EPNs seems to be due to the rapid proliferation of the nematode symbiotic bacteria within the ticks, since the nematodes do not go through their natural cycle within ticks, and most infective juveniles die shortly after entry (Mauleon, Barre & Panoma, 1993; Samish, Alekseev & Glazer, 1995; Hill, 1998; Kocan *et al*. 1998*b*; Hassanain *et al*. 1999). *In vitro* experiments demonstrated that tick hemolymph hinders the growth of EPNs (Zangi, 2003), but the reason(s) for nematode mortality within ticks is/are not yet fully understood. Interestingly, when the cuticle of *I. scapularis* was physically slit before nematode infection, the nematodes *S. carpocapsae* and *S. glaseri* reproduced successfully (Zhioua *et al*. 1995).

Laboratory assays. Ticks exposed to nematodes in Petri dishes lined with moist filter paper showed that six genera of Ixodidae and two genera of Argasidae were readily killed by entomopathogenic nematodes (Table 1). Only *B. microplus* appeared to be resistant to nematode attack (Mauleon *et al*. 1993). Various tick stages differ substantially in their susceptibility to EPNs, with the fully engorged female ticks being most susceptible and the pre-imaginal stages least sensitive. During feeding, ticks were highly resistant to EPNs and their eggs were totally resistant. Unfed

Table 1. Effects of entomopathogenic nematodes upon various tick species (Petri-dish tests)

Ticks		Nematodes			Susceptibility of tick stages						
							Engorged females				
							LC_{50}		LT_{50}		
Genus	Species	No. of strains tested	Most virulent: Species	Most virulent: Strain	Engorged nymphs	Unfed adults	Nematodes/ cm^2	On day post infestation	Days	Nematodes/ cm^2	Reference
Amblyomma	*americanum*	5	*S. riobrave*	TX			<35	20			Kaaya *et al.* 2000
	cajennense	1	*S. riobrave*	TX			>180	20			Kaaya *et al.* 2000*b*
	gemma	4	*S. carpocapsae*	DT	+		250	14			Kocan *et al.* 1998*b*
	maculatum	1	*S. riobrave*	TX			>180	20			Kocan *et al.* 1998*a*
	variegatum	21	*S. carpocapsae*	Mex	+(−)	+(−)	20	14			Mauleon *et al.* 1993 Osir *et al.* unpublished Samish *et al.* 1995, 2000*b* Samish & Glazer, 1992
Boophilus	*annulatus*	7	*H. indicus*	IS-5	+	+	<2·6	8	1·9	10	Mauleon *et al.* 1993
	–''–	12	*H.* sp.	RD4					1·0	40	Samish & Glazer, 1998, 2000*b*
	decoloratus	4	*S. riobrave*	HP88			<50	14			Kaaya *et al.* 2000*b*
	microplus	14	None		−	−	Not susceptible		Not susceptible		Mauleon *et al.* 1993
Dermacentor	*variabilIis*	2	*S. riobrave*	HP88			>180	20			Kocan *et al.* 1998*a*
Hyalomma	*dromedarii*	5	*S.* sp.	S1	+		50	7	7	50	El-Sadawy & Habeeb, 1998
	excavatum	5	*H. indicus*	IS-5	+	+			2·8	250	Samish *et al.* 1999*b*, 2000*b*
Ixodes	*scapularis*	15	*H. megidIis*	M145	−	−	20	10	2·0	250	Hill, 1998; Zhioua *et al.* 1995
Rhipicephalu	*appendiculatus*	5	*S. riobrave*	HP88	+	+	<50	14			Kaaya *et al.* 2000
	bursa	5	*H.* sp.	IS-3					5·0	250	Kocan *et al.* 1998*a*
	evertsi	5	*S. carpocapsae*	DT	+	+	<50	14			Osir *et al.* unpublished
	sanguineus	7	*S. riobrave*	HP88	+	+	>180		3·2	250	Samish *et al.* 1999, 2000 Samish & Glazer, 1992 Samish *et al.* 1999*b*
Argas	*persicus*	3	*H. bacteriophora*	HP88	+	+	70	3	<1·3	420	Hassanain *et al.* 1999
Ornithodoros	*moubata*	3	*S. carpocapsae*	DT	+				2·3	10	Samish *et al.* unpublished
	tholozani	4	*S. carpocapsae*	DT	+						

Abbreviations: Nematode genera: *S.* = *Steinernema*; *H.* = *Heterorhabditis*; + susceptible; − not susceptible; LC_{50} and LT_{50} concentration and time, respectively, required to kill 50% of the ticks.
Modified after Samish & Glazer (2001).

female ticks were killed up to six times quicker (LT_{50} 1 d for *R. bursa*) than engorged ticks (6 d for *R. bursa*) (Samish *et al.* 2000*a*, *b*; Table 1). This may be connected to the strong anti-bacterial activity of the tick haemolymph (Ceraul *et al.* 2002).

The many strains of more than 25 nematode species from the families Heterorhabditdae and Steinernematidae display a wide range of characteristics, enabling them to adjust readily to the various different pests in different ecological niches. The 42 nematode strains tested for anti-tick activity showed varying degrees of virulence (Table 1). In laboratory tests, heterorhabditid nematodes were generally more virulent to ticks than steinernematids (Mauleon *et al.* 1993; El-Sadawy & Habeeb, 1998; Hill, 1998; Hassanain *et al.* 1999; Glazer *et al.* 2001). Nematode strains virulent to one tick stage of one species were found, in most cases, to be also highly virulent to other tick species and stages (El-Sadawy & Habeeb, 1998; Hassanian *et al.* 1999; Samish *et al.* 1999*a*, *b*).

Field trials. The virulence of nematode strains to ticks as measured in Petri dish tests in the laboratory often differs considerably from that measured in field trials when the nematodes are sprayed on soil. The difference could result from the specific behaviour of each nematode strain in the soil environment, e.g. how deep in the soil they prefer to live, how they react to UV irradiation, low moisture or other factors.

Among nine strains of three nematode species tested against *B. annulatus* ticks on soil, under simulated field conditions, the commercial S*teinernema carpocapsae* Mexican strain was the most effective: a nematode dosage of 50/cm^2 of this strain killed 100% of the engorged females with a LT_{50} of less than 5 days (Samish *et al.* 1999*a*).

Environmental conditions strongly influence the pathogenicity of nematodes to ticks. Soils with a high silt concentration or with more than 25% (v/v) manure were found to reduce the anti-tick activity of EPNs relative to that measured on clean sandy soil (Samish *et al.* 1998, 1999*a*). The anti-tick activity of EPN strains also varied with temperature (Zhioua *et al.* 1995): the optimal activity for most strains was 25–28 °C, although some displayed far wider ranges of activity (e.g. 18–34 °C; unpublished observations). EPNs sprayed on humid sandy soil 3 days before ticks were added killed 100% of the ticks, whereas EPNs sprayed on soil containing 25% (v/v) cattle manure resulted in 45% mortality, and on soil containing 40–50% silt only 25% mortality (unpublished observations). EPNs sprayed on soil covered with leaf litter or grass were highly efficient in killing ticks compared with those sprayed on uncovered soil. Shading the soil with nets (10–90% shade) and irrigating it twice a day increased tick mortality from nematode attack in comparison with that on unshaded soil or on plots irrigated only once every 2 days (Zangi, 2003).

Nematodes are potentially useful tools for tick control because: (1) engorged ticks are susceptible to some EPNs and also reside in locations that are preferred by many nematode strains; (2) immobile ticks attract mobile nematodes; and (3) spraying or irrigation can be easily used to apply nematodes to a tick habitat. However, the use of nematodes may be limited to defined ecological niches because their pathogenicity is reduced by low humidity or temperature, high concentrations of manure or silt, and by differences in the susceptibility among the various tick stages and species. The wide genetic variation found among the many nematode strains, and presumably in strains yet to be found, means that genetic manipulation of nematodes could increase the range of ecological conditions in which they could be successfully applied against ticks. The development of improved formulations is also important. Finally, in-depth studies are needed to elucidate the interactions between nematodes and ticks under field conditions.

PARASITOIDS

Most parasitoids used in the biological control of insect pests of plants belong to the order Hymenoptera. This is the dominant order among entomophagous insects, both numerically and in regard to their successful use in biological control. Over two-thirds of the cases of successful biological control of pest species have been achieved with hymenopteran parasites (De Bach & Rosen, 1991).

Only a few species of hymenopteran parasites are known to affect ticks. L. O. Howard first described two species of chalcidoid wasps collected from ticks in Texas (Howard, 1907, 1908). These are now both included in the genus *Ixodiphagus* of the family Encyrtidae, which includes seven species, all tick parasites (Trjapitzin, 1985; Davis, 1986; Mwangi *et al.* 1997).

The most widespread species is *I. hookeri* (synonyms, *Hunterellus hookeri*, *I. caucurtei*; see Gahan, 1934; Trjapitzin, 1985) which has been recorded from Asia, Africa, North America and Europe (Hu, Hyland & Mather, 1993). Other species have been reported from these continents and also from Australia (Oliver, 1964; Doube & Heath, 1975; Graf, 1979; Mwangi & Kaaya, 1997). Collection of *I. theileri* from a specimen of the tick *H. rufipes* that was attached to a migrating bird in Egypt (Kaiser & Hoogstraal, 1958) suggests a possible mode of long-distance transport for these wasps. Most species of *Ixodiphagus* are host-generalists, which have been collected from a variety of hard tick species (Oliver, 1964), and in at least one case (*I. mysorensis*) from soft ticks (*Ornithodoros* sp.) (Mani, 1941). Nevertheless, some degree of host preference has been reported (Bowman, Logan & Hair, 1986). *I. hookeri* uses tick odour cues to find hosts (Takasu *et al.* 2003).

Nymphal ticks were parasitized while they were engorging on vertebrates (Smith & Cole, 1943), and parasitoid egg development was found to be associated with ingestion of blood by its host tick (Hu & Hyland, 1998).

The only species that has been released for biological control of ticks is *I. hookeri*. Larrousse *et al.* (1928) released *I. hookeri* (propagated from wasps originally collected in France) on Naushon Island off the coast of Cape Cod, Massachusetts, USA, in 1926. The parasites were released as adults, in parasitized *I. scapularis* nymphs, and on mice (with parasitized nymphs attached). Infected nymphs of the target species, *Dermacentor variabilis*, were collected the following summer, which suggests that the parasite overwintered successfully. The ticks were less common the year after the parasite was released, but both *D. variabilis* and *I. scapularis* remained common at the site 12 years later, even though the parasite was still present (Cobb, 1942). Smith & Cole (1943) released about 90 000 female *I. hookeri* at two sites on Martha's Vineyard, Massachusetts, but found no evidence of parasite persistence or of tick control. Mwangi *et al.* (1997) released about 150 000 specimens of *I. hookeri* over a 1 year period to control *Amblyomma variegatum* on a field with 10 infested cattle in Kenya. They reported a reduction in tick numbers from 44 to 2 ticks per animal, suggesting that inundative releases can provide tick control at individual sites.

One possible explanation for this pattern can be surmised from recent surveys for *I. hookeri* in southern New England and New York (USA). This species is present on Naushon Island (MA), Prudence Island (RI), Bridgeport and Bluff Point Coastal Preserve in Groton (CT) and on Shelter Island and Fire Island (NY), all sites with extremely dense populations of the tick *I. scapularis*. However, the wasp is rare or absent at nearby sites with fewer ticks (Hu *et al.* 1993; Stafford, Denicola & Magnarelli, 1996; Ginsberg & Zhioua, 1999). Furthermore, sharp and sustained reductions in deer populations that lowered tick numbers at sites in Connecticut (USA) resulted in sharply lowered rates of *I. hookeri* parasitism as well (Stafford *et al.* 2003). Thus, it appears that *I. hookeri* requires high tick densities to persist in the northeastern US and is not likely to provide tick control under natural conditions. Nevertheless, inundative releases to control ticks in limited areas (e.g. farms, recreation areas) are still potentially feasible (Mwangi *et al.* 1997). Furthermore, Knipling & Steelman (2000) argued, on the basis of a simple theoretical and economic analysis, that parasitoids have a high potential as biocontrol agents for *I. scapularis*. They pointed out that a successful application would require a substantial research effort on parasitoid taxonomy, ecology and behaviour, and an inexpensive production system would be needed (e.g. artificial media for cultivating parasitoids) to produce large numbers of parasites for release. *I. hookeri* can be reared in large numbers in the laboratory at a modest cost in countries with low price labour (Mwangi & Kaaya, 1997), but the need to maintain large numbers of ticks and vertebrate hosts could be problematical for commercial production. If additional research confirms the efficacy of parasite release for tick control on individual farms or over broader areas, then improved parasite production methods would have to be developed.

Interestingly, Mather, Piesman & Spielman (1987) found that the *I. scapularis* parasitized by *I. hookeri* on Naushon Island did not carry the pathogen *Borrelia burgdorferi* (causative agent of Lyme borreliosis) and rarely carried *Babesia microti* (agent of human babesiosis), even though these pathogens were common in uninfected ticks at that locale. Thus, wasp infestation might lower pathogen prevalence in ticks, even if it does not control tick numbers. However, the lack of infection in parasitized ticks might have resulted from preferential parasitization of ticks attached to white-tailed deer (Stafford *et al.* 1996; Hu & Hyland, 1997), a large, conspicuous host that is not a competent reservoir for either pathogen. Furthermore, pathogen-infected ticks are still abundant at many sites where these wasps are present, so wasp parasitism does not, by itself, control the risk of disease. Further study is needed to determine whether wasp infestation influences pathogen infection in ticks.

Ixodiphagus spp. parasitize only ticks, as far as is known. Therefore, non-target effects would presumably be minimal if these parasites were released for tick control. The likely susceptibility of these hymenopteran parasites to many agricultural insecticides would require careful coordination to avoid interference between pesticide applications and parasitoid releases. At present, the lack of efficacy in nature, insufficient information on the efficiency of inundative release and the unknown cost of a parasitoid control programme renders the use of this means for tick control in the near future unlikely.

PREDATORS

Many tick bio-suppressors such as ants, beetles and many bird species are general predators that feed occasionally on ticks, therefore their populations do not depend on the sizes of the tick populations. General predators can sometimes affect the size of a tick population in nature, but manipulating their populations to reduce tick numbers would require large increases in the predator population, which could also cause large changes in populations of non-target species in natural areas (Symondson, Sunderland & Greenstone, 2002). Therefore, general tick bio-suppressors will not be covered in this chapter.

Avians

Some 50 bird species have been reported to eat ticks (Petrischeva & Zhmayeva, 1949; Mwangi *et al*. 1991*a*; Samuel & Welch, 1991; Petney & Kok, 1993; Verissimo, 1995; Samish & Rehacek, 1999). However, only a few species seem to feed specifically on ticks, and thus only a few would be expected to have a meaningful effect on tick populations.

Chickens. Chickens (*Gallus gallus*) confined with cattle in Africa were reported to ingest an average of 338 ticks per bird during 5·5 h. Other experiments found that the birds ate from 9·7 to 81 ticks per bird per hour of foraging. At high tick concentrations, an average of 69% of the ticks were consumed by chickens (Hassan *et al*. 1991; Hassan, Dipeolu & Munyinyi, 1992; Dreyer, Fourie & Kok, 1997). Chickens are neither tick-specific predators nor obligatory predators, therefore their consumption of ticks depends largely on alternative food availability and the density of the tick population. Thus, chickens are unlikely to reduce tick densities below a certain level. Nevertheless, chickens maintained in any case on small mixed farms can help to reduce tick populations at nearly no cost.

Oxpeckers. *Buphagus africanus* (the yellow-billed oxpecker, YBO) and *B. erythrorhynchus* (the red-billed oxpecker, RBO), both native to Africa, are the only birds known to feed specifically on ectoparasites, especially ticks. Oxpecker populations have decreased along with reductions in the numbers of game animals, increased use of bird-poisoning acaricides and possibly also decreased tick populations (Robertson & Jarvis, 2000; Van Someren, 1951; Stutterheim & Stutterheim, 1980; Stutterheim & Brooke, 1981). However, oxpecker reintroduction efforts, an increase in game animals and the introduction of safer acaricides appear to have resulted in increases in these bird populations during the last two decades.

Stomach contents of captured oxpeckers included 16 to 408 ticks per bird (Van Someren, 1951; Bezuidenhout & Stutterheim, 1980). The consumption by young RBOs of larval, nymphal and adult *Boophilus* ticks averaged 1176, 1549 and 1293, respectively, during 6–7 days of exposure to tick-infested cattle. This result was extrapolated to adult RBOs as the equivalent of 12 500 larval or 98 engorged *B. decoloratus* females. YBOs can consume about 10% more ticks than RBOs (Bezuidenhout & Stutterheim, 1980; Stutterheim, Bezuidenhout & Elliott, 1988).

Oxpeckers are visual predators, first plucking the engorged females, then searching large body areas and scissoring and eating the smaller tick stages. YBOs prefer foraging on buffaloes and white rhinos, whereas RBOs prefer other ungulate hosts. Oxpeckers prefer feeding on weak mammals and will feed repeatedly on specific individuals within the same herd, with preference for the hosts with most ticks (Van Someren, 1951; Mooring & Mundy, 1996). *Buphagus* birds may also feed on skin, pieces of meat and blood of the mammalian host; thus they may enlarge wounds or even open partially healed wounds, although most publications suggest that such behaviour is quite rare (Bezuidenhout & Stutterheim, 1980; Stutterheim *et al*. 1988; Weeks, 1999). The YBO was found to be more aggressive than the RBO.

Several programmes have attempted to reintroduce oxpeckers artificially into areas from which they had previously disappeared (Davison, 1963; Couto, 1994; Grobler, 1976, 1979). Oxpeckers are difficult to propagate in captivity and reintroduction programmes were based on translocation of birds that were captured in the wild. When enough birds were translocated, the oxpeckers established themselves successfully, and calf mortality from tick burdens was reduced (Couto, 1994).

For a successful oxpecker introduction programme, a number of problems must be considered (Mundy & Cook, 1975; Couto, 1994; C. Foggin personal communication). The tick population should be monitored to assess the importance of the birds and the success of the introduction programme. A suitable location to capture the oxpeckers is needed (e.g. where they feed on tame calves) – mist nets can be used to capture the birds. Oxpeckers are social birds, therefore a minimum of 20 birds is recommended for translocation. It is important to overcome panic among cattle and game animals in the new location when they first encounter the oxpeckers. The new release area should have a suitable climate and should be at least 10 km away from areas treated with bird-poisoning anti-ectoparasitic compounds. Amitraz or pyrethroid-based dips do not seem to be harmful. The new area should include at least 500 head of game animals or of undipped domestic animals, grazing on at least 3000 ha.

Oxpeckers seem well suited to play an important role in IPM programmes for the control of ticks. However, their major value will be as only one part of a broader integrated programme, because substantial tick populations are known to remain in areas populated with oxpeckers (Masson & Norval, 1980; Norval & Lightfoot, 1982).

CONCLUDING REMARKS

The development of anti-tick biological control agents (BCAs) is still in its infancy. Furthermore, the various steps required for commercialization of these products, including adaptation by companies (production, storage and delivery) and education of consumers (storage, application and evaluation of results), are still in the future. Nevertheless, we believe that the need to develop alternative control

methods, and the increasing, though still small, number of scientists working on anti-tick BCAs will yield useful results.

The fact that some BCAs and particular strains are far more specific in their selection of target pests than are acaricides (in some cases, specific to individual stages of a given tick species) and that many strains are effective only under specific ecological conditions, provide considerable advantages over pesticides, because harmful ecological effects are minimized. However, the specificity of some BCAs might require that numerous anti-tick BCAs be developed to deal with tick infestations in different environments.

Partial or total replacement of chemical acaricides with inundative use of tick pathogens and/or parasitoids would require considerable changes in the techniques of producers and suppliers. Products would probably need to be developed for specific small or medium-sized markets, including more pest-specific products with relatively short shelf lives, and quicker-reacting suppliers. The commercial success of such tailor-made control methods may require on-site instructors or even controllers, with the necessary specific knowledge (which may need to be far more comprehensive than that required to use pesticides). Furthermore, clients will have to accept the slower activity of BCAs compared with chemical controls. Commercial viability might vary, depending on the specific pest, the adaptability of BCA-based approaches, and the availability of other effective management techniques.

Biological control of plant pests, by means of parasitoids, predatory mites, viruses, *B. thuringiensis*, bugs, beetles, and others, has had several striking successes. These include the use of several enemies/pathogens simultaneously or in a pre-determined order. However, only about 5% of all pest problems are treated with biological control methods (Van Dreisch & Bellows, 1996) and many problems have to be solved in order to increase their use (Wysoki, 1998). Relatively few studies have been performed on the existence of promising natural enemies of ticks, or on their use against ticks in most parts of the world. Collaboration between biocontrol experts who have experience in managing plant pests and tick experts could lead to valuable developments in tick biocontrol.

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