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BIOLOGY AND CONTROL OF CATTLE GRUBS¹

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PERSPECTIVES AND OVERVIEW

Two species of cattle grubs (Diptera: Oestridae) affect cattle in the Northern Hemisphere: *Hypoderma lineatum*, the common cattle grub or lesser cattle warble fly, and *Hypoderma bovis*, the northern cattle grub or larger cattle warble fly. The word *warble* is Anglo-Saxon for boil.

Adults of the cattle grub are commonly known as heel flies, warble flies, bomb flies, or gad flies. This parasite has been observed and recorded for centuries (159), and Bracy Clark (50) cited and discussed references from Biblical times to Shakespeare. Scientific observations on the biology were first recorded in the 1700s by Vallisnieri (cited in 224) in Italy, followed by an extensive review and taxonomic description by Brauer (34) in Austria in the mid 19th century. Major contributions followed in England by Ormerod (157) and Imms (93); in the United States by Riley (179), Osborn (158), Bishopp et al (24), and Mote (132); and in Canada by Hadwen (85). Other reviews completed before the widespread use of systemic insecticides for cattle-grub control include work by James (94) and Scharff (185) in the United States, Gansser in Austria (69), Gebauer in Germany (70), Grunin in Russia (81), Natvig in Norway (141), MacDougall in Scotland (124), and Bevan & Edwards (22) in England. The quality of these reviews makes it unnecessary to repeat detailed information about the stage descriptions and life cycles for these two important species. Rather, I attempt to summarize these contributions, emphasizing additions to our knowledge since the 1950s.

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BIOLOGY

Life Cycle and Damage

Female *Hypoderma* spp., which are bee-like in appearance (85), use a specialized ovipositor (75, 133) to attach their eggs to host animal hairs by means of an attachment organ (51), which is an outgrowth of the egg chorion. The most often selected site of attachment are hairs on the legs and lower body regions of cattle (83). The body temperature of the host animal aids in incubation of the eggs, which is normally 3–7 days (24). Newly hatched larvae (~1 mm in length) (42), crawl to the base of the hair shaft and penetrate the host (43) by means of proteolytic enzymes secreted from their blind midgut (115, 142). Occasionally, edema and inflammation occur at the penetration site, most often with older, previously infested animals (73). Once inside the host, the first-stage larvae migrate for 4 to 6 months, normally through the fascial planes between muscles, along connective tissue (86), or along nerve pathways (35), again aided by proteolytic enzymes secreted from the anterior part of the migrating larvae (26). Digestion by the larvae is transcuticular (48); enzyme action aids in the transport of nutrients into the hemolymph. *Hypoderma lineatum* larvae travel forward to the resting site (12, 17) in the loose submucosal connective tissue of the esophagus (88, 199). *Hypoderma bovis* larvae move to a similar resting site in the epidural fat between the dura mater and periosteum in the region of the thoracic and lumbar vertebrae of the spinal canal (220). During the period when larvae accumulate in sizable numbers in their resting sites, treatment with systemic insecticides is contraindicated because of the possibility of adverse reactions due to inflammation from large numbers of grubs being killed in a confined area. Typical symptoms with *H. lineatum* are bloating or vomiting (101, 186), and with *H. bovis*, the reaction may be manifested as temporary posterior paralysis (57, 100, 134, 135).

Eventually, the late first-instar larvae (~15 mm in length) of both species leave their respective resting sites, move to the middorsal region of the host (86), and position themselves just under the skin (201). Here they open respiratory holes in the skin and evert with their posterior spiracles toward the breathing pore (70). A cyst then begins to form around each larva. The total migration time of larvae from egg hatch to arrival at the back is 8 to 9 months. The damage done to cattle hides by the presence of large numbers of these pores (149) has been the major economic loss due to *Hypoderma* infestation (10, 66, 92, 127, 150, 222).

The cyst-like furuncles, or warbles, are of host origin (4, 84). Here the larvae dramatically increase in size (from 15 to 30 mm) through two molts for a period of 30 to 60 days. Larvae inside the warbles live in a relatively stable environment (145) of inflammatory exudate (147) and depress second-

ary infection by production of bacteriostatic substances (15, 95). After the mature larvae exit, healing of the skin opening is rapid (126). Carcasses from slaughtered cattle with severe infestations must often be trimmed drastically to remove the jellied fat and meat tissue located beneath the warbles (166, 177).

Immediately prior to exiting the warble, the grubs become distinctly darkened (97, 192), and the fully mature larvae exit their warbles through the pores. These still-motile larvae drop to the ground, crawl under leaf litter or burrow near the surface in loose soils (40, 198), pupariate (128), and undergo pupal metamorphosis for another 30–90 days, depending on temperature and humidity (164).

The adults (11–18 mm in length) emerge from the puparium through an operculum and immediately crawl to where their wings can harden and expand. The adults are aphotaxous (20, 184) and must mate and reproduce solely on the energy derived from stored reserves. Their life span is normally 3–5 days, but they can live 10–15 days under laboratory conditions (79). For mating, adults aggregate at sites in steep-banked draws or stream beds (46, 69). Hybridization is probably prevented by temporal and spatial separation of the two species, and attempts to produce hybrids by laboratory mating have been unsuccessful (216). The males wait at the sites for females to fly through to copulate (46). Females normally mate only once, although multiple matings are possible (216). The females emerge with a fully developed complement of 300–650 eggs (193), and unlike most other Diptera, they do not require a postfertilization pause to mature their eggs (213). Female *Hypoderma* spp. have two unique adaptations that help compensate for their short, aphotaxous life span. The first is the initiation of oogenesis in the late third-instar larvae in the warbles (25, 193). The second is the simultaneous development of two oocytes within the same ovariole, thus doubling the reproductive capacity (193).

Following copulation, the females search for a suitable host. Oviposition between the two species also differs. *H. lineatum* normally deposit eggs in long, connected strings, often while the host animal is at rest (44); *H. bovis*, however, oviposits eggs singly by darting in and attaching each egg on an individual hair shaft (24). The persistent activity and buzzing by the latter species causes cattle to gad, an agitated, instinctive flight response of cattle to the presence of an ovipositing *H. bovis* female (84, 85). Injury and miring of fleeing cattle, spontaneous abortion, reduced milk production (178), delayed breeding, and the increased labor necessary to regather stampeded cattle are all potential but, to date, unassessed losses due to gadding (84, 175). The fly has no apparatus to cause pain, either in the form of piercing mouthparts or a sting, so the intensity and cause for this exaggerated response are still not completely understood (146).

The question of reduction in weight gain attributable to *Hypoderma* spp. infestation is still open to interpretation. Several studies reported that parasitism by *Hypoderma* spp. larvae caused marked reduction in weight gain (83, 106, 122). In determining the total impact of arthropods on livestock production, Drummond et al (65) reported more than \$600 million annual losses due to cattle grubs in the United States, excluding the cost of control. Drummond (62) later analyzed 26 trials that measured average daily gain and reported that at least half of the trials showed no treatment advantage, and he revised his annual loss figures to \$66 million, still excluding the cost of control. In a Canadian study, Scholl et al (191) measured the production effects of cattle grubs on beef cattle with no control and found no discernible difference in several beef production values among cattle with 2–39 grubs. Many questions remain unanswered, such as the threshold level of infestation that causes economic loss, interaction with environmental stress, effects of other parasitic infections (especially endoparasites), and the appetite-enhancement effect of some treatments.

Life-Stage Description

In addition to the review articles above and those citations that give specific taxonomic descriptions (94, 152, 161, 221, 224), the following specific references to life-stage structure and function have been published.

CHROMOSOMES Both *H. lineatum* and *H. bovis* have six pairs of chromosomes with a diploid number of 12 (33, 112).

EGGS The structure and function of *Hypoderma* spp. eggs have been described (51) with emphasis on the specialized basal attachment organ.

LARVAE In-depth descriptions of *Hypoderma* spp. larvae have included the internal organs (56), the digestive tract (26), the Malpighian tubules (137), hemocytes (138, 203), the larval cuticle (54, 58, 96, 97), cuticular sensillae (52, 98), spiracles and respiration (45, 53, 63, 136, 139, 144, 192), and the initiation of gonotrophic development in the late third-instar larvae (25, 143, 193).

ADULTS Structure and function of the genitalia (75, 133, 160), tarsal sensillae (55), mating behavior and mating site selection (46, 80, 213, 215, 216), flight (49, 146), and population dynamics (9, 36, 37, 39, 108, 129–131) of adult *Hypoderma* spp. have been described.

Hosts

Zumpt (224) hypothesized that the original host(s) of these two species of *Hypoderma* were extinct bovids once found in the warmer regions of Asia or Europe. Both species were probably introduced to North America in beef and

dairy cattle (*Bos taurus*) imported from Europe (221) and subsequently infested bison (*Bison bison*), the only nearctic native animal in which these two *Hypoderma* species have been reported (121, 182). Additionally, they have been reported infesting closely related bovids such as yaks (38), and water buffalo and zebu cattle (140). A closely related species, *Hypoderma* (= *Oedemagena*) *tarandi*, the caribou warble fly, is holarctic in distribution (221). Other animal hosts parasitized by *H. lineatum* and *H. bovis* include horses (82, 151) and sheep and goats (174), and there are numerous reports of human myiasis (59, 113, 196). In these incidental hosts, *Hypoderma* spp. do not complete development and, therefore, have little effect on fly population levels. A report of completed larval development in an equine host (223) has not been repeated. Trials involving transplantation of first-instar larvae into recipient animals (18) failed to show alternate host suitability. Investigators infecting laboratory mice (71) and rabbits (32) with *Hypoderma* spp. larvae were successful only when they first immunosuppressed the host.

Distribution

H. bovis and *H. lineatum* occur naturally in cattle in at least 50 countries in North America, Europe, Africa, and Asia between 25 and 60° latitude in the Northern Hemisphere (123). The southern limit is reached in the Punjab of India (202), Libya (19), northern Mexico (76), and Hawaii (1). Cattle grubs have been introduced into the Southern Hemisphere in imported cattle (11, 148, 204, 218), but it is unlikely that any ever established indigenous populations there (224).

In the U.S., *H. lineatum* ranges from northern Mexico to northern Canada, while *H. bovis* is found north of a line running west to east from northern California through Kansas to the Carolinas (24). A small recurring population of *H. bovis* has been reported in central Florida (74).

The distribution of the two species in North America has remained essentially unchanged since the early part of the century (23). Larvae leaving the host during moderately cold weather are not destroyed by the direct effect of environment (164); they have a very wide tolerance range for cold (183) and diverse soil conditions (198). Susceptibility of puparia to high temperatures may be the factor limiting the southward distribution of *H. bovis* (165, 215). However, the indirect effect of climate on activity and viability of biotic agents such as arthropods, bacteria, and fungi may play a greater role than previously thought (188).

CONTROL

Chemical Control

Of the nearly 1400 citations reviewed for this article, more than 30% dealt with chemical control techniques and results. Drummond et al (64) and

Berkenkamp & Drummond (21) described the development of chemical control of cattle grubs in the U.S., and similar reviews have been presented for Canada (99) and Great Britain (13).

Area-Wide Control

The advent of systemic organophosphorus insecticides in the 1950s gave cattle producers the first opportunity to control cattle grubs on a large scale at a reasonable cost. Prior to this, cattle grubs were controlled by manual expression of second- and third-instar larvae from warbles or by the application of chemicals such as rotenone to the backs of animals to kill larvae in their warbles. The development of systemic insecticides provided an opportunity to kill migrating larvae prior to their arrival at the backline and thus avoided the damage done to hide and meat in that region. Because this strategy was prophylactic rather than reactive, proposals were made to eradicate *Hypoderma* spp. on a large scale using systemics alone (77). Coincidentally, however, researchers around the world were discovering that a combination of producer reluctance and biological rebound capacity were making such eradication schemes almost impossible to achieve (176, 210). Some maintained that vigilance and mobilization were all that were necessary (102a, 222a). The Province of Alberta in Canada and several European countries attempted concerted efforts to eradicate *Hypoderma* spp. Authors summarizing these attempts in Europe (31, 219) opined that much more remained to be done before this goal could be realized. Only Great Britain has faced the problem with complete and continuing government support in a national effort (205–207). The failure to elicit 100% cooperation from producers and dependence on a single strategy has led to the conclusion that cattle-grub control would be best approached with an integrated management program (109, 153).

The first attempt at integrated management of *Hypoderma* spp. resulted from the suggestion (46, 78) to adapt the sterile male–release technology that was developed for eradication of the screwworm (*Cochliomyia hominivorax*) from North America. The results of a preliminary trial in Alberta, Canada (214) were very encouraging, and consequently, the Joint U.S.–Canada Cattle Grub Project (110, 217) was initiated in 1982. The chemical reduction phase proved to be very successful using readily available systemic insecticides combined with 100% producer cooperation (189). Even though there was a strong indication that releases of sterile males eliminated *Hypoderma* populations from the release zones, the objectives of the sterile fly component proved to be more difficult to achieve (111) due to the overwhelming logistical problems inherent with an insect for which there was no efficient technique for large-scale *in vitro* rearing (14). Nevertheless, an economic evaluation of the project demonstrated cost effectiveness, in spite of the difficulties encountered with production of sterile males (106).

Avermectins

Perhaps the most promising control technology for use in eradication of *Hypoderma* spp. has been the development of the group of pharmaceuticals known as the avermectins. The first to be developed and tested for efficacy against cattle grubs and other parasites of cattle was Ivomec® from Merck (41, 114, 167). By the early 1980s this antiparasitic compound was being hailed as one of the most effective materials ever developed for systemic use against cattle grubs (60, 104). Despite concerns about possible environmental consequences from its use (212), Ivomec® possesses unique characteristics not seen in organophosphorus systemics. The first of these is an ability to kill migrating larvae, but unlike systemics, it is also highly efficacious against second- and third-instar larvae in warbles (105). The latter activity permits use of this material as a late-season (194) or pour-on (2) treatment for grub-infested cattle that is not possible with traditional systemic insecticides, which are ineffective once the larvae are inside their warbles. Additionally, Ivomec® produces 100% mortality of migrating *Hypoderma* larvae of both species at dramatically low dosage levels (3, 61). However, because it is used against a wide range of internal and external parasites, the lowest effective dilutions could lead to problems of resistance and reduced efficacy with other target species (114). Other avermectins in development that have already demonstrated similar efficacy against *Hypoderma* spp. are Moxidectin® from American Cyanamid (190) and Doramectin® from Pfizer.

Biological Control

A review (188) of the few references pertaining to biological activity against *Hypoderma* spp. concluded that despite the scarcity of relevant literature, both distribution and population densities of cattle grubs might be more affected by parasites, predators, and pathogens than previously thought.

Immune Response and Vaccines

Hadwen & Bruce (87), Koegel (107), and Peter (163) reported anaphylaxis in animals injected with macerated *Hypoderma* larvae. This anaphylactic reaction is similar to the results of treatment with systemic insecticides when migrating larvae are concentrated in their resting sites in the esophagus and spinal canal regions (102). Antigenic material from the hemolymph of the larvae or the material released by the disintegration of larvae killed by insecticide reacts with antibody in the tissues of the host and produces an allergic reaction with concomitant symptomology (16, 28).

Generally, fewer *Hypoderma* spp. larvae appear in the back of older cattle than in calves or yearlings (24), which implies the development of some type of immunity with age. The internal host-parasite regulating mechanism (129) probably has its origin in the host immune response system (67, 72). As early

as the 1920s, researchers in France (181) and Germany (162) suggested using crude extracts of *Hypoderma* larvae to immunize animals. In Japan, efforts were made to characterize the toxic substance extracted from *Hypoderma* larvae, which Japanese researchers called hypodermatoxin (89–91, 154–156, 209). Simmons described the proteolytic activity associated with extracts of *H. lineatum* larvae (200) and the histopathological changes in the tissues of parasitized animals (199, 201).

Major advances have occurred in the past 15 years in the study of the biochemistry of *Hypoderma* digestive enzymes and of the bovine immune response to cattle-grub infestation. Four protease fractions have been isolated and described: hypodermin C or collagenase (8, 27, 30, 115, 117, 118, 120), hypodermin A (211), hypodermin B (119), and P2 (195). The amino acid sequence of hypodermin C has been reported (116), and hypodermin A messenger RNA has been prepared from first-instar larvae of *H. lineatum* (208). A potential parasite-induced immunosuppressive mechanism by the degradation of host complement protein C3 by the hypodermins A and B was reported (5, 29). Descriptions also have been reported of the antigenicity and immunogenicity of *H. lineatum* proteins in rabbit (32) and bovine hosts (168, 173), and of the shared epitopes between the soluble proteins of *H. lineatum* and *H. bovis* (172).

Initial investigations using extracts of *Hypoderma* spp. larvae as candidate vaccines (7, 103, 125, 169, 180, 197) have led to concerted attempts toward the development of a defined vaccine against cattle-grub infections. Instead of extracts from collected larvae, these defined vaccines have focused upon the principal protein antigens of first-instar larval *H. lineatum*, hypodermins A, B, and C. Hypodermin A has been evaluated in pure form (47, 68, 170, 171), and the other hypodermins in various combinations (6, 171).

The advantages of a vaccine over chemical control are great: less damage to the environment, complete and lifetime conversion of susceptible animals to resistant status, and use in animals such as dairy cattle for which systemic insecticide application is prohibited during lactation, to name a few. Experimental vaccine efficacy has been manifested as an increase in total *in vivo* larval parasitic mortality. Experimental vaccines have not, to date, protected the subcutaneous tissues of the back and prevented hide damage in individual animals by significantly increasing mortality in migrating larvae. However, because of the increase in mortality to those larvae arriving at the back, current experimental vaccines are designed to increase overall larval mortality and therefore reduce the levels of *Hypoderma* spp. populations. However, these experimental vaccines have not been field-tested against naturally occurring populations of *Hypoderma*. If population reduction can be achieved, the lower efficacy of vaccines presumably will require

a longer period of time to reach acceptable levels of control than has been observed with conventional chemical control technology. Thus, experimental vaccines already developed may have limited value for use in intensive control programs designed to reduce the cattle-grub population drastically over a short period of time (47). Vaccines may, on the other hand, be useful in less intensive control programs and as a complement instead of a substitute for chemical control in integrated management programs. If acquired immunity can be maintained for the life of the animal and herd immunity maintained by vaccination, dramatic and rapid cattle-grub population growth as a result of withdrawal of or reduction in chemical control pressure may be greatly retarded or maintained at subeconomic levels. Because vaccines do not elicit the complete efficacy that systemic insecticides do, we may need to redefine long held concepts relating to economic thresholds and control. Finally, the increased understanding of the cattle immune response system as it interacts with *Hypoderma* spp. has far-reaching implications for other host-parasite relationships.

During the past several years, the prevalence of both *Hypoderma* species has declined dramatically (187) in North America. This is especially true of *H. bovis*, which has all but disappeared west of the Mississippi River (D. D. Colwell & J. E. Lloyd, personal communication). The cause(s) for this decline is (are) unknown. Possibly the widespread use of systemic insecticides, especially the avermectins, on and in range and feedlot cattle in this region, or changes in the environment, have driven the population of *H. bovis* below an undefined critical level.

Improved, safer insecticides combined with advances in the understanding of *Hypoderma* spp. biology and ecology and of the bovine immune system interacting with these parasites may have finally put control or even eradication of the two *Hypoderma* species within reach. To achieve sustained control or eradication, the interest of producers and researchers in cattle-grub biology and control must remain high for at least the next decade.

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