Ecobiology of the sheep nose bot fly (Oestrus ovis L.): a review

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SUMMARY

The sheep nose bot fly, Oestrus ovis L. (Diptera: Oestridae) is the causal agent of a very common cavitary myiasis affecting sheep and goat hosts worldwide. We reviewed the biology of the parasitic (feeding larvae) and free (non-feeding intrapuparial and adult) living phases as related to individual intrinsic and environmental factors. Temperature is the main environmental factor regulating the life cycle of this organism during both the parasitic and free phases. First-stage larvae are thought to be responsible for monitoring environmental cues inside the host nasal passages. By contrast, second and third-stage larvae accumulate nutrient body reserves in order to support the intrapuparial and adult periods. Based on literature, this paper reports the first life table for an O. ovis population. Under natural conditions, the rate of population growth was 1.25 per generation, which indicates a great capacity of populations to recover from internal and external adverse factors. Interfering with water and fat accumulation during the parasitic growth phase of this organism may be a promising new approach for designing control measures.

Keywords: Cavitary myiasis, developmental biology, Oestridae, Oestrus ovis.

RéSUMÉ

Ecobiologie de l’oestre du mouton (Oestrus ovis L.): revue bibliographique

Oestrus ovis L. (Diptera: Oestridae) est un parasite cosmopolite responsable d’une myiase des cavités nasales et des sinus frontaux du mouton et de la chèvre. Les particularités biologiques des stades parasites qui s’alimentent et des stades libres qui ne s’alimentent pas (pupe et adulte) sont en étroite relation avec des facteurs individuels intrinsèques et des facteurs environnementaux. La température est le principal facteur environnemental régulant le cycle évolutif d’O. ovis aussi bien pendant sa vie parasitaire que pendant sa vie libre. Les larves du premier âge jouent un rôle important dans le contrôle des réactions de l’hôte pendant leur séjour dans les cavités nasales. En revanche, les larves du second et du troisième âge accumulent des nutriments corporels en vue de la phase pupale et de la vie adulte. Elles s’appuyant sur la littérature, cette synthèse récapitule les caractéristiques biologiques des populations d’O. ovis. Dans les conditions naturelles, la croissance de la population est de 1,25 par génération ce qui montre une grande capacité à récupérer face aux facteurs défavorables internes et externes. Pour l’avenir, une voie originale de lutte serait d’interférer avec le métabolisme de l’eau et l’accumulation des réserves lipidiennes dans les larves perturbant ainsi le stockage des réserves destinées aux stades libres qui ne s’alimentent pas.

Mots clés : Myiase cavitaire, biologie du développement, Oestridae, Oestrus ovis.

Introduction

The sheep nose bot fly (Oestrus ovis L.) causes a severe cavitary myiasis in practically all sheep and goat producing areas of the world. It is currently considered as a very well-adapted parasitic organism which is hard to fight or to eradicate [25]. Oestrosis impairs the wellbeing and performance of the hosts, affecting growth, wool and milk production [22]. As happens with other cold-blooded organisms, this parasite is highly dependent on external cues for initiating and maintaining developmental and reproductive cycles [10]. The larval (parasitic) phase of the life cycle plays two primary roles, i.e. it is the feeding phase when all the body reserves are acquired [15]. These reserves are essential to support the metamorphic and reproductive processes which are carried out during the free (non-parasitic phase) of the cycle [20]. Larval stage is also the main responsible for regulating the developmental rhythms that ensures the population survival inside and outside the host [40]. Both, the free-living intrapuparial and adult stages are responsible for species adaptation and for maintaining the highest population reproductive rates [8, 19]. Renewed interest in O. ovis populations has been helpful to understanding relevant ecobiological aspects often neglected or poorly understood for years. The purpose of this paper was i. To integrate recent knowledge on the biology and ecology of O. ovis and ii. To identify population reproductive aspects potentially important for the control of this parasite.

Biology of larval stage

ESTABLISHING MECHANISMS

First-stage larvae are larviposited in packages directly into the nostrils with amazing precision. Each larval package consists of a sticky bundle of immobile, longitudinally arranged larvae that become activated in contact with the air and host temperature. The size of each larval shot depends on the degree to which the fly is spent. For example, packages of 24 (fresh flies) to 3 (spent flies) larvae were recorded [18]. The last three abdominal segments of the female fly act as a larvipositing

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“gun” structure. The gonopore opening is located between the VII and VIII abdominal segments, among especially-arranged sclerites [12]. The larvipositor is normally telescopically retracted so the the vaginal duct should be extended when larvae are expelled. The wall of the uterus is highly tracheated and muscular so uterus contraction may be important for helping the larval packages to be ejected. Thermo sensible cuticular sensilla [23] and a quick mobility allow them to identify the right direction and colonize the nasal cavity in seconds, overcoming the first defensive reactions such as sneezing and rubbing against close objects. Most of them reach the nasal cavity in a few seconds, but occasionally some migrate externally and die desiccated in a few minutes. Reported observations indicate that the range of L1 establishment rate is 0-48% in sheep [24, 26] and 29-40% in goats [3]. It is known that sheep provide a more suitable environment for larval early establishment and development than do goats [24, 35, 2], but behavioral defensive mechanisms may also influence the rate of larval establishment, since goats are much more reactive to larvipositing fly presence. Furthermore, water economy is better developed in goats; therefore, their noses are usually less humid than in sheep. This higher humidity may help the larvae to survive more easily in sheep [14]. The L1 stage lasts from less than 10 days to more than 25 days under favorable temperatures [12].

Inside the host’s nose, the larvae continue growing or go into hypobiosis as a response to a combination of intrinsic rhythms and external environmental signals.

HYPOBIOsis in First instars

During the cold season of temperate countries, first instars hosted by animals undergo hypobiosis [30, 43], but very high temperatures also slow down the growth rate. In the summer of the Baja California Peninsula, extreme temperatures (＞38°C) delayed the growth of L1 larvae, which extended up to six weeks or more in sheep (Cepeda and Angulo, unpublished data). ROGERS et al. [38] failed to demonstrate that air temperature of the L1 larval overwintering site is the direct cause for the hypobiotic response. However, experimental evidence showed that first-stage larvae undergo hypobiosis signs (mechanical fixation by oral hooks on the nasal mucosa, absence of motile reflexes) at refrigerating temperature (5°C in vitro) and can be maintained alive for several days without any nourishment. Forward locomotion was recovered at 12°C and vigorous locomotion, foraging behaviors were acquired after warming up (15-18°C), and they were capable of quick movements and strong foraging behavior at 19-22°C. We therefore assumed that L1 larvae stay in the nasal cavity because they need to monitor the external air temperature. Also, in order to gain as much heat as possible from the host, L1 larvae posses a structure more flattened than L2 or L3 larvae. The width/height ratio in somatic cross sections was 2.5 in L1 and 1.8 in L2 larvae. Thus, the larval temperature resulting from the host-larva-environment exchange system should be over the threshold necessary for activation of L1 larval metabolism for growth. In temperate areas, this threshold should be reached during the spring and the summer.

Favorable in vitro average temperatures above 19°C seems to be crucial to continue developing to molt. First instars usually molt to the second instar before entering the frontal bone cavities and rarely molt in the frontal sinuses. After the first molt, the growth process is continuous [9]. Larval transnasal migration through the pharynx has been observed. In such cases, up to 65% of larvae may colonize the contralateral nasal cavity [12, 42]. Frequently, L3 larvae mature at the same time in groups of 3-8 that leave the host within a few days. Second- and third-instars share the frontal base cavities so competition for surface fixation sites on the host’s mucosa and feeding is evident, especially in highly infected hosts.

Intrapuparial development

Mature L3 larvae leave the host to pupariate in the soil. After leaving the host, a fresh, dry shaded area is necessary for safe pupariation and intrapuparial development. The wandering larvae must be careful in selection of the place to dig and pupariate since it is during this phase that they are very susceptible to damage and/or predation. A thick (0.5 mm) puparial wall provides protection and permits gas exchange. Posterior and lateral trachea connect the respiratory system of the insect to the internal pupal wall. After pupal-adult apolysis, the pharate adult is not tracheally connected to the puparial wall, and gas exchange is then achieved through the puparium.

As with other oestrids, intrapuparial development is highly dependent on temperature that regulates the metamorphosis process [34, 8]. About 243 degree-days are necessary for development in males and 279 for females [10]. Individuals can withstand transitory temperatures of as high as 45°C for short periods during the day. However, weight losses are accelerated resulting in delayed eclosion (seven weeks or more) when pupae are exposed to persistent high temperatures. Under these conditions, weak adults and defects may occur [11]. It appears that high temperatures are deleterious because unavoidable puparial weight losses are increased [12]. During this period, weight losses are also important for adult survival [11], since lightweight flies (for example, 60 mg or less) die within a few days under laboratory and field conditions. Mortality of developing individuals during the intrapuparial period may be significant. Mortality rates of 41-100% have been observed, depending on the rearing temperature [39, 10, 11]. Under laboratory conditions, females emerge 22 d and males 21 d after pupariation. Alternating high and low temperatures during the day seem to be beneficial to enhance survivability. Increasing temperature during the morning may be a proper signal for emergence since most flies emerge during the morning [12]. During the intrapuparial period, normally 82% of larval weight is lost [20]. At emergence, water and fat reserves were 76.5, 12.3 mg in females and 75.4, 11.6 mg in males, respectively [13]. Thus, during both larval-pupal and pupal-adult metamorphoses, individuals lost about 77% of water and 65% of fat reserves acquired during the larval stage.

Reproductive intrapuparial events

After sinking in the soil, the prepupal stage coincides with tanning and hardening of the outer cuticular layers. Intrapuparial ovarian maturation begins in females after the pupal-adult
apophasis. Yolk deposition begins at the yellow-eye stage and continues during the rest of the pharate adult stage. At emergence, females possess a complement of fully developed eggs, one per ovariole, ready to be fertilized. Females produce 337-652 eggs [21], which is comparable to other oestrid species of high reproductive rates. In males, spermatogonia undergo mitotic divisions and form sperm cysts during the cryptopheal pupal stage (24-72 h postpupariation). When head eversion occurs, primary spermatocytes begin undergoing meiosis and secondary spermatocytes appear during the apophasis pupal-adult.

The second meiotic division and spermiogenesis processes prevail from the transparent-eye stage until emergence. At emergence, testes were full of free sperm, sperm bundles and developing cysts in some cases [17].

**Larval growth, water and fat accumulation**

Growth during the first instar is poorly understood. When L1 larvae reach 4.3 mm in length they advance to the middle turbinate bones where they molt to L2 stage and enter the frontal sinus cavities. Here, the L2 go through a variable growth period and molt to L3 when 11.5 mm size is reached [15]. Growth rates expressed in weight gains are the highest during the early L3 period. Recently, fat and water composition in L2 and L3 larvae was studied [13]. L2 larvae accumulated mostly water during this period. Water content increased significantly during the early L2 period from 52.3% to 77.8% in late L2. By contrast, up to 49% of fat and 28% of the post-fed larval water reserves are stored during the early L3 period. On the average, each mature post-fed L3 larva had an average complement of 33.4 mg of fat and 368 mg of water. It is not known the existence and nature of intra-host regulatory mechanisms for larval establishment and growth. Parasite-controlled mechanisms in addition to host defenses both are necessary to avoid overcrowding the nasal cavities. From necropsy observations and vaccination using L3 products [26] or using L3 intestinal hidden proteins, ANGULO-VALADEZ et al. [4] discussed the existence of possible intra-host regulatory mechanisms exerted by L2 and L3 larvae vs. L1 establishment and growth.

Mature female L3 larvae tend to be heavier (0.511g) than male larvae (0.489g) [16], but no other external morphological differences have been reported. Within the species parameter range, there are relationships between larval weight with pupal survival and adult size. Data analysis from laboratory and field-reared specimens showed that survival during intrapupal and adult periods may be compromised when larval growth is affected. At a larval mature weight reduction of 40%, a reduction of 38% of the adult population is expected to occur [16].

The parasitic and free phase developmental stages found at necropsy provide valuable information about the total population. A high percentage of recently-deposited larvae indicate a high adult infective activity, while a high percentage of quiescent larvae suggests seasonal hypobiosis. A high percentage of L2 in a given population suggests a very dynamic developmental continuum that reflects favorable environmental conditions for *O. ovis*. Accumulation of high percentages of maturing L3 larvae may be useful in forecasting the proximity of an adult emergence surge 1-3 months later.

**Adult stage**

After emergence, flies have a limited lifespan before dropping protein, energy and water reserves. Average water and fat reserves of brown-eyed pharates were 76.5, 12.3 mg in females and 75.4, 11.6 mg in males, respectively [13]. Newly emerged adults must find a sexual partner for mating. Aggregation sites of gravid females have been described [6, 28], but the specific sites for mating and mating characteristics are largely unknown. After a few days of larval incubation, larvipositing females resume the life cycle, infecting new hosts to initiate future generations. Following fertilization, under laboratory conditions embryogenesis and full larval development is completed in about 12 days [19]. Later on, gravid females must locate an appropriate host. Visual and olfactory mechanisms for long-range host location are thought to be involved. The visual range of *O. ovis* flies seems to be rather short and highly dependent on daylight intensity as was observed under field conditions (unpublished data). During field tests (unpublished) gravid tethered flies were allowed to orientate freely toward walking adult goats. On a clear, sunny day (solar irradiance 1200 w/m²) visual range of gravid flies was 7 m. Visual range decreased to 3.5 m under semicloudly and 2 m under cloudy conditions.

**Host location for larviposition**

From field tests, it was shown that carbon dioxide, octenol, and acetic, propionic and butyric acids released from sheep or goat dummies were unable to attract wild gravid females [18]. Recently, PODDIGHE et al. [36] reported that the antennae of adult *O. ovis* females are well developed, and posses several types of olfactory sensilla of trichoid, basiconicum and coeloconica types. These authors also showed the ability of female flies to detect synthetic odor compounds such as dimethyl trisulphide (DMTS), hexanoic acid and NH₃. Solutions of 1% DMTS, 10% ammonia and 1-hexanol were effective olfactory stimuli for *O. ovis* females [36] so these or related compounds may be involved in long-range host location.

Infective flies are very skillful at locating the nose of the host. Analysis of risk factors showed that dark-muzzled sheep may be more attractive for larviposition [33, 5]. Also, altitude, latitude, flock size, and host population density were the potential risk factors associated with the presence of *O. ovis* [1]. The nature of the stimulus for long and short-distance host detection is not known, however, optic stimulus from potential hosts such as walking herd groups may attract the flies from moderate distances. Shape and movement of the host’s head appear to be important at short distances to elicit the reflex of larviposition. Active gravid flies were able to larviposit on mobile ovine and caprine dummies with no chemical stimulation [18]. From field observations made by the authors, after long-distance host location, infective flies remained close to
the flock. Traveling on the host’s back or horns, flies struck the free-ranging flock until their larval reserve was depleted. Depletion of the larval reserve coincides with depletion of nutrient somatic reserves. In the morning, flies become activated only when temperatures are above 12-18°C. Below this range, they are unable to fly and remain dormant. However, under warm and dry conditions, the optimum temperature for larviposition is between 25-28°C. It is plausible that the ambient temperature influences and synchronizes both the larvipositing female and L1 larval metabolisms for the critical life-cycle steps of larviposition and L1 establishment. Flies can larviposit at noon or at dusk light intensities even under light gusts of wind, but this activity is suppressed below 20ºC and at high temperatures above 35°C, probably because flies are unable to dissipate the excess of energy generated during flight, as happened in walk-in cage tests for fly larviposition stimulation [18].

**O. ovis population dynamics**

Populations of oestrids in the wild have been little addressed in the literature. Populations studies so far available for *O. ovis* were reported by MELENEY et al. [32] and MELENEY and APODACA [31]. However, most published papers on *O. ovis* populations deal mainly with epidemiological aspects [e.g. 29, 1, 27]. The lack of field techniques for trapping and monitoring adults and very complex ecological characteristics of these species are probably the main causes. WEINTRAUB [41] published a life table for the common warble fly (*Hypoderma lineatum*) in Canada. These reports were based on systematic toxicological treatments applied to cattle in an isolated area in New Mexico. After five years, average larval burden decreased from 49.8 in 1958 to 8.7 in 1962. Discontinued control efforts resulted in full population regeneration three years later. New and published data on *O. ovis* mortality enabled us to construct a life table shown in Table 1. Mortality rates during the egg and newly-laid L1’s and during the post-fed and intrapuparial phase were very important. However, the highest mortality rate is expected to occur during the larval stage. Using mathematical approaches, BART and MINÁR [7] demonstrated that mortality rate was the highest during the L1 period. Intrapuparial and adult mortality were also important causes of population depletion. When natural causes were the only forces acting on a *O. ovis* population, the number of parasitic individuals grew in a given area at a rate of 1.25 which is somewhat close to the 1.5 reported for *Hypoderma lineatum* [41]. These data indicate that populations of this parasite have a great ability to recover from adverse factors and that integrated management is necessary to eliminate sheep botfly populations. It is important to consider that when population growth rate equals 1 the population is in balance, and when it is below 1, the population is decreasing [37]. In addition, fighting the larval phase alone will never be enough to eliminate the population.

**General Conclusion**

Rhythms of *Oestrus ovis* development and reproduction are highly governed and synchronized by environmental factors. Among them, temperature is the most important environmental signal regulating the entire life cycle. Temperature regulates intrapuparial development and adult activity as well. Inside the host, L1 larvae living in the host nasal cavities seems to play a specific role of monitoring external temperature. The highly growing stage L2 and L3 are responsible for water and fat accumulation, respectively, to withstand the free phase of the life cycle. New data on ecobiology of *O. ovis* is useful in understanding very complex life cycle steps such as mating and host location. Affecting the accumulation of water and energy reserves during the larval phase appears to be a promising approach for reduction of adult populations.

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### Table 1: Life tables for *O. ovis*, under natural conditions and absence of control measures

<table>
<thead>
<tr>
<th>Age interval</th>
<th>Individuals alive</th>
<th>Main cause of death</th>
<th>Individuals dying</th>
<th>Mortality rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg and newly-laid L1</td>
<td>500</td>
<td>Failures in fertilization, fly inability to strike a proper host</td>
<td>200\textsuperscript{DI}</td>
<td>40</td>
</tr>
<tr>
<td>Developing larva inside the host</td>
<td>300</td>
<td>Host immune reactions</td>
<td>210\textsuperscript{DD}</td>
<td>70</td>
</tr>
<tr>
<td>Post-fed larva and intrapuparial mortality</td>
<td>90</td>
<td>Predation, bad weather, death during metamorphosis</td>
<td>54\textsuperscript{DI}</td>
<td>60</td>
</tr>
<tr>
<td>Adult</td>
<td>36</td>
<td>Bad weather, disiccation, predation</td>
<td>11\textsuperscript{DI}</td>
<td>30</td>
</tr>
<tr>
<td>Total remaining individuals</td>
<td>25 (12.5 females)</td>
<td>Infertility, inability to find a mate</td>
<td>11.38\textsuperscript{DI}</td>
<td>91</td>
</tr>
</tbody>
</table>

\textsuperscript{1}Specific assumptions and references for table construction. Egg production/female or maximum biotic potential=500 (Babcock, 1953; Breev, 1975); In uterus egg and newly-laid L1 mortality 40% (Cepeda et al., unpublished data); Larval mortality 70% (Angulo et al., 2007); pre-pupal and intrapuparial mortality 60% (Loos, 1989; Cepeda et al., 1998). Emergence-larviposition adult mortality 50% (Cepeda unpublished data); rate of unfertilized females 91% (Babcock, 1953); Carrying capacity (number of potential host) Not limiting; Female fly cohort to follow One Female: male ratio 50:50.

\textsuperscript{2}Host density dependent (\textsuperscript{DD}), host density independent (\textsuperscript{DI}).
References


