Oestrus
(insect: dipteran)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Diptera (true flies) have two pairs of wings, but the hindwings are reduced to stabilizing halteres. All species are holometabolans and exhibit complete metamorphosis whereby vermiform larval stages undergo pupation and transform into free-flying adults. Several major parasitic groups are recognized: nematocerans (small slender bodies, long filamentous antennae, narrow wings) and brachycerans (larger bodies, short stout antennae, broad wings); the latter being divided into the Tabanomorpha (larval head capsule sclerotized) and the Muscomorpha (larval head not sclerotized, circular-seamed (cyclorrhaphous) pupae). Muscomorphans include the glossinids (tsetse flies), hippoboscids (louse flies), muscids (house flies), calliphorids (blow flies), sarcophagids (flesh flies) and oestrids (bot flies); all with sponging or biting mouthparts. These flies are either ectoparasitic with adults biting hosts (former three groups) or endoparasitic with vermiform larvae developing in host tissues (latter three groups). Oestrids (bot flies) are large hairy flies but they are not parasitic as adults. Their larvae (bots) are obligatory endoparasites in the integumentary, respiratory or digestive tracts of animals, and they exhibit a high degree of host specificity. Four subfamilies are recognized: cuterebrines (skin bots), oestrines (head maggots), gasterophilines (stomach bots) and hypodermatines (cattle grubs/warbles). Oestrine larvae of *Oestrus* spp. develop in the nasal passages and sinuses of hoofed animals causing considerable pain.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum:	Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class:	Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder:	Holometabola (Endopterygota) (young do not resemble adults, pupae, with internally developing wings)
Order:	Diptera (true flies, single pair of forewings, hindwings modified into halteres, vermiform larvae)
Suborder:	Brachycera (tabanid/March flies, short stout antennae often with aristae, telmophagy)
Infraorder:	Muscomorpha (Cyclorrhapha) (flies, cyclorrhaphous (circular-seamed) pupae, larval head not sclerotized)
Division:	Schizophora (head with frontal suture (lunule))
Section:	Calyptratae (calypters cover halteres)
Family:	Oestridae (large hairy bot flies, third larval stage or bot resemble small sausages, larvae cause myiases)
Subfamily:	Oestrinae (head maggots)
Genus:	*Oestrus* (parasitic in nasal sinuses of sheep)
Species:	various species cause nasopharyngeal myiases

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Flies are small winged holometabolans that undergo complete (holometabolous) metamorphosis with vermiform larvae undergoing pupation in silk cocoons. Thousands of dipteran species have been described throughout the world, most being free-living saprophages (detritivores) but some being parasitic either as adults biting and feeding on hosts (often haematophagous) or producing larvae that invade host tissues (condition known as myiasis). Two major suborders are recognized: the Nematocera (with small bodies, long filamentous antennae, narrow wings and aquatic larvae and pupae); and the Brachycera (with large bodies, short stout antennae often with aristae and broad wings).

Major parasitic dipteran families	Biodiversity	Parasitic stages	Status	Pathogenesis*	Disease transmission
Suborder: Nematocera (small midges/mosquitoes, thread-horned with long filamentous segmented antennae (= nemato-cera), aquatic life-cycles (larval/pupal stages associated with water), female adults require blood meal before they can lay eggs) (34 families)					
Culicidae (mosquitoes)	3 subfamilies, 70 genera, 3,500 species	adult ♀	obligate	blood-sucking	viral, protozoal, helminth
Psychodidae (moth flies, sand flies)	5 subfamilies, 150 genera, 3,000 species	adult ♀	obligate	blood-feeding	viral, bacterial, protozoal
Simuliidae (black flies)	3 subfamilies, 30 genera, 2,000 species	adult ♀	obligate	blood-feeding	protozoal, helminth
Ceratopogonidae (biting midges)	4 subfamilies, 110 genera, 6,000 species	adult ♀	obligate	blood-feeding	viral, protozoal, helminth
Suborder: Brachycera (large tabanid/March flies, with stout and fewer antennal segments (= brachy-cera), antennae often with aristae, females with slashing-sponging mouthparts to pierce skin and feed on pool of blood (telmophagy)) (120 families)					
Infraorder: Tabanomorpha (larval head capsule incomplete posteriorly (only anterior parts sclerotized))					
Tabanidae (horse flies, deer flies)	3-5 subfamilies, 133 genera, 4,300 species	adult ♀ [+ larvae]	obligate [accidental]	blood-feeding [GI, UG, TR myiasis]	viral, bacterial, protozoal, helminth
Infraorder: Muscomorpha (Cyclorrhapha) (aristate antennae, setose bodies, cyclorrhaphous pupa)					
Section: Calyptratae (calypters cover halteres)					
Superfamily: Muscoidea (synanthropic flies)					
Muscidae (house flies, stable flies)	9-10 subfamilies, 190 genera, 4,200 species	adult ♀, ♂ [+ larvae]	obligate [accidental]	biting, blood-feeding [CU, GI, TR myiasis]	bacterial, helminth
Superfamily: Oestroidea (cause larval myiases) (6 families)					
Calliphoridae (blow flies)	11 subfamilies, 75 genera, 1,100 species	larvae	facultative, obligate	CU, GI, NP, AU, UG TR, myiasis	-
Sarcophagidae (flesh flies)	3 subfamilies, 108 genera, 2,500 species	larvae	facultative, obligate	TR, GI, CU myiasis	-
Oestridae (bot flies, warble flies)	5 subfamilies, 25 genera, 150 species	larvae	obligate	CU, GI, NP, OC myiasis	-
Superfamily: Hippoboscoidea (pupa-bearers)					
Glossinidae (tsetse flies)	1 genus, 3 species-groups, 25 species	adult ♀, ♂	obligate	blood	protozoal
Hippoboscidae (louse flies, keds)	1-3 subfamilies, 21 genera, 212 species	adult ♀, ♂	obligate	blood	viral, protozoal, helminth

*type of myiasis: AU = auricular; CU = cutaneous; GI = gastro-intestinal;
NP = naso-pharyngeal; OC = ocular; TR = traumatic; UG = uro-genital.

The suborder Brachycera contains 6 infraorders: Asilomorpha (bee flies, robber flies, spider flies), Muscomorpha (previously suborder Cyclorrhapha) (house flies, blow flies, fruit flies), Stratiomyomorpha (soldier flies), Tabanomorpha (horse, deer and snipe flies), Vermileonomorpha (wormlions) and Xylophagomorpha (awl flies); all of which vary considerably in their morphological and biological characteristics. Members of the infraorder Muscomorpha differ from the others in that they form cyclorrhaphous (circular-seamed) pupae (adults eclose through a circular cap rather than a longitudinal slit), larvae without sclerotized heads, and adults with short pendulous 3-segmented antennae (the third segment often bearing feather-like aristae), palps with a single segment, and feet with 2 pads. Collectively, 15 superfamilies have been classified into 2 Divisions: the Schizophora (containing flies whose heads bear a frontal ptilinial suture and sclerotized lunule); and the Aschiza (hover flies lacking a frontal suture and lunule). Within the Schizophora, 2 sections are recognized: the Calypterae (comprising flies with calypters covering the halteres, large squamae, a strong thoracic suture and well-defined grooves on the antennal pedicels); and the Acalypterae (without covering calypters, small squamae, a weak thoracic suture and no pedicel grooves). Calyptratae flies are divided into 3 superfamilies: Muscoidea (synanthropic flies with well-developed sponging mouthparts for feeding on decaying organic material or biting mouthparts for blood-feeding, most females being oviparous (egg-layers)); Hippoboscoidea (louse flies and tsetse flies with elongate biting mouthparts for blood-feeding, female flies formerly regarded as pupa-bearers and placed in group Pupipara (now defunct) as they have since been shown to birth mature larvae (considered to be prepupae)); and Oestroidea (blow flies, bot flies and flesh flies whose larvae are endoparasitic and cause myiases). Several superfamilies contain species whose larvae feed on the flesh of vertebrate hosts, mostly when dead (carrion) but sometimes when still living (causing fly-strike). Oestroid and muscoid larvae are well-adapted for living in moist organic substrates ranging from wet faeces to carrion to living flesh.

The superfamily Oestroidea is characterized by relatively large flies that are not dorsoventrally flattened, their wing veins are not crowded, and the discal medial cell of the wings widens gradually. The superfamily contains 7 families: Calliphoridae (blow flies); Oestridae (bot flies); Polleniidae (cluster flies); Rhinophoridae (woodlouse flies); Sarcophagidae (flesh flies); Tachinidae (parasitic flies); and Ulurumyiidae (McAlpine's fly). The family Oestridae (bot flies, also known as warble flies, heel flies, gad flies) form large hairy adult flies with bulbous heads, small antennae, rudimentary mouthparts, and wings with subcostal veins running parallel to the costa before joining it. Females produce eggs which hatch by discarding an anterodorsal cap, releasing vermiform larvae which are endoparasitic in the tissues (skin, digestive tract or respiratory passages) of vertebrates. The first larval instars have thorn-like spines encircling several segments, while second and third instars have ecdysal (moulting) scars around their spiracular plates (characteristic for the family Oestridae). Over 150 species have been described in some 25 genera in 5 subfamilies: Cephenemyiinae (deer bot flies), Cuterebrinae (New World skin bot flies), Gasterophilinae (stomach bot flies), Hypodermatinae (Old World skin bot flies, warble flies), and Oestrinae (nose and throat bot flies); with one unplaced genus and 3 fossil genera. Representative genera of veterinary significance are tabulated below:

Oestrid subfamily	**Genera**	**Hosts**	**Strike**	**Myiasis***
Cuterebrinae (New World skin bot flies)	*Dermatobia*	cattle, humans	primary	Obligate (CU)
Oestrinae (nose and throat bot flies)	*Oestrus*	sheep	primary	Obligate (OC, NP)
Hypodermatinae (Old World skin bot flies, cattle grubs, ox warbles, heel flies)	*Hypoderma*	cattle	primary	Obligate (CU)
Gasterophilinae (stomach bot flies)	*Gasterophilus*	equines	primary	Obligate (GI)

*type of myiasis: CU = cutaneous; GI = gastro-intestinal; NP = naso-pharyngeal; OC = ocular.

The subfamily Oestrinae contains 9 genera (*Cephenemyia, Cephalopina, Gedoelstia, Kirkioestrus, Oestrus, Pharyngobolus, Pharyngomyia, Rhinoestrus, Tracheomyia*); all being viviparous flies that deposit or forcibly eject packets of larvae onto the muzzle or eyes of vertebrate hosts. The larvae migrate into the nasal cavities and may cause nasopharyngeal myiases. The genus *Oestrus* (syn. *Aestrus, Cephalemya, Cephalemyia, Cephalomyia, Estrus, Oestreus*) contains 8 species that infect domestic livestock (especially sheep and goats) as well as some wild ungulates (antelope, deer) and occasionally animals and people in close contact (such as sheep dogs, shepherds, farmers). Infections are usually temporary as the third stage larvae leave their hosts to undergo pupation in the soil. Nasal and throat bots are cosmopolitan in distribution, and are widespread throughout Africa and central Asia.

Oestrus* species	**Hosts**	**Location**	**Clinical signs**	**Distribution**
O. aureoargentatus (syn. *O. regalis*)	Artiodactyla: bovid (sable antelope, roan antelope, topi, tsessebe, hartebeest, Lichtenstein's hartebeest, blue wildebeest)	nasal passages	obligate myiasis	Africa
O. caucasicus (incl. *O. gvozdevi*)	Artiodactyla: bovid (ibex, Pyrenean ibex, Siberian ibex, Caucasian tur)	nasal passages	obligate myiasis	Central Asia
O. curvicauda	Perissodactyla: equid (horse)	nasal passages	obligate myiasis	Europe
O. dubitatus	Artiodactyla: bovid (blue wildebeest)	nasal passages	obligate myiasis	Africa
O. halensis	Artiodactyla: bovid (sheep)	nasal passages	obligate myiasis	Europe
O. macdonaldi (syn. *O. bassoni*)	Artiodactyla: bovid (hartebeest)	nasal passages	obligate myiasis	Africa

O. ovis (syn. *O. argalis, perplexus*) (sheep nasal bot)	Artiodactyla: bovid (sheep, Lacaune sheep, argali, bighorn, goat, ibex), camelid (camel), cervid (white-tailed deer); Carnivora: canid (dog); Primates: hominid (human)	nasal passages, eyes	obligate myiasis (nasal discharge, sneezing)	worldwide
O. variolosus (syn. *O. bertrandi, disjunctus, interruptus*)	Artiodactyla: bovid (topi, tsessebe, bontebok, hartebeest, Lichtenstein's hartebeest, sable antelope, gemsbok, blue wildebeest)	nasal passages	obligate myiasis	Africa

*The species *O. cervi* and *O. elaphi* described from deer have been transferred by most authorities to the genus *Cephenemyia*

Parasite morphology: *Oestrus* spp. form 4 different types of developmental stages: eggs (*in utero*); larvae (3 instars); pupae (in puparia); and adults (males and females). Eggs appear as elongate bodies approximately 1 mm long which are surrounded by thin translucent shells and are retained within the uterus of female flies. The eggs hatch releasing larvae which are subsequently birthed by larviposition. The larvae (called bots, sometimes grubs) are robust, cylindrical tapering at both ends, and become somewhat flattened ventrally as they mature. They develop through 3 instars (L1-3) growing from 1-2 mm to 12-20 mm and then up to 20-35 mm in length. They are initially white in colour but become yellow-brown with dark transverse bands on each segment (they do not become completely black like Hypodermatinae and Cuterebrinae). The segmented body lacks fleshy projections but bears numerous small spines mostly clustered together in ventral patches on most segments (unlike muscoid larvae which lack spines). Larvae lack sclerotized head capsules but have internal cephalopharyngeal skeletons with prominent rasping mouthparts containing well-developed dark curved mandibles (oral hooks). The caudal segment also bears 2 sets of 10-11 posterior hooks (crochets) located on terminal protuberances. The larvae respire through posterior spiracles located on 2 caudal black circular plates (not indented) with numerous openings (pores) arranged in radial ray patterns (in contrast, cuterebrine larvae have plates with 3 slits containing numerous openings, while calliphorid larvae have plates with 3 slits surrounded by a sclerotized peritreme). In *Oestrus* spp., anterior spiracles are absent or obscure, posterior spiracles on L1 are rudimentary, those on L2 have <100 pores, and those on L3 have >100 pores. Plates on L2 and L3 also encloses a button-like ecdysal (moulting) scar which is characteristic for most Oestridae. Mature L3 leave the host and form puparia which are robust dark-brown barrel-shaped bodies 20-30 mm long. The enclosed pupae transform into adult flies which eclose through circular caps (like all Cyclorrhapha) and not through longitudinal slits (like Nematocera and Brachycera). Adults are large heavy-bodied flies 10-19 mm long with grey-brown bodies that appear mottled due to patchy coverings of short brown hairs (but lacking stout bristles). They have bulbous broad heads flattened front-to-back that are dull yellow in colour but randomly covered with black glossy pits. Their heads possess both a ptilinal suture and facial lunule (like other Oestroidea and Muscoidea, but unlike other calyptrate flies). They have 2 small yellowish compound eyes located laterally and separated by a large frons with small wart-like protuberances (tubercles), and 2 small antennae sunken into pits on the face, each composed of 3 dissimilar segments: a short basal scape; a club-like pedicel with a complete dorsal seam; and an anterior flagellum comprising a single large slender bristle (arista) which is bare (like those of Hypodermatinae, but unlike those of Cuterebrinae which are plumose). Adult flies have small and inconspicuous mouthparts, reduced to small knobs and lacking palps. Adult flies do not feed but live on energy stores acquired as larvae. The alimentary tract is also rudimentary, but may possibly be used for water uptake and fluid regulation. The thorax is covered by a shield-like scutum with a posterior lobe-like scutellum bearing small black tubercles. The dorsal scutum often bears four black parallel stripes composed of tiny hairs. Like other oestroid flies, there is a vertical row of bristles on the thoracic meron (lacking on muscoid flies). The mesothorax bears one pair of small clear wings whose membranes are supported by 6 primary veins [costa (C), subcosta (Sc), radius (R), media (M), cubitus (Cu), and anal (A)], with the Sc vein running parallel to the C vein, and the M vein not reaching the wing margin directly but joining the R vein. Similar to all Diptera, the hindwings have been reduced to small club-like halteres used to stabilize flight. The halteres are covered by posterobasal lobes of the forewings (squamma or calypters) which are typically large in oestrids (except gasterophilines). Adults also have bulbous swellings (greater ampullae) below their wing bases like other oestrids. The ventral thorax is the point of attachment for 3 pairs of short robust yellow hairy legs, each composed of 5 segments (coxa, trochanter, femur, tibia, and tarsus) with the tarsal portions covered with strong bristles and all legs terminating in a pair of claws with pad-like pulvilli surrounding a central bristle (empodium). The segmented abdomen usually appears globular with a shiny integument lightly covered in hairs. The terminal segments are modified by genital structures, including a copulatory aedeagus in males and a cylindrical telescoping larvipositor in females. Male flies have 2 testes with vas deferens leading to a seminal vesicle (with lateral accessory glands) feeding into a tubular ejaculatory duct linked to the aedeagus and claspers. Female fliers have 2 ovaries connected by oviducts to a globular uterus (with associated spermatheca and accessory glands) leading to the vulva and terminal larvipositor.

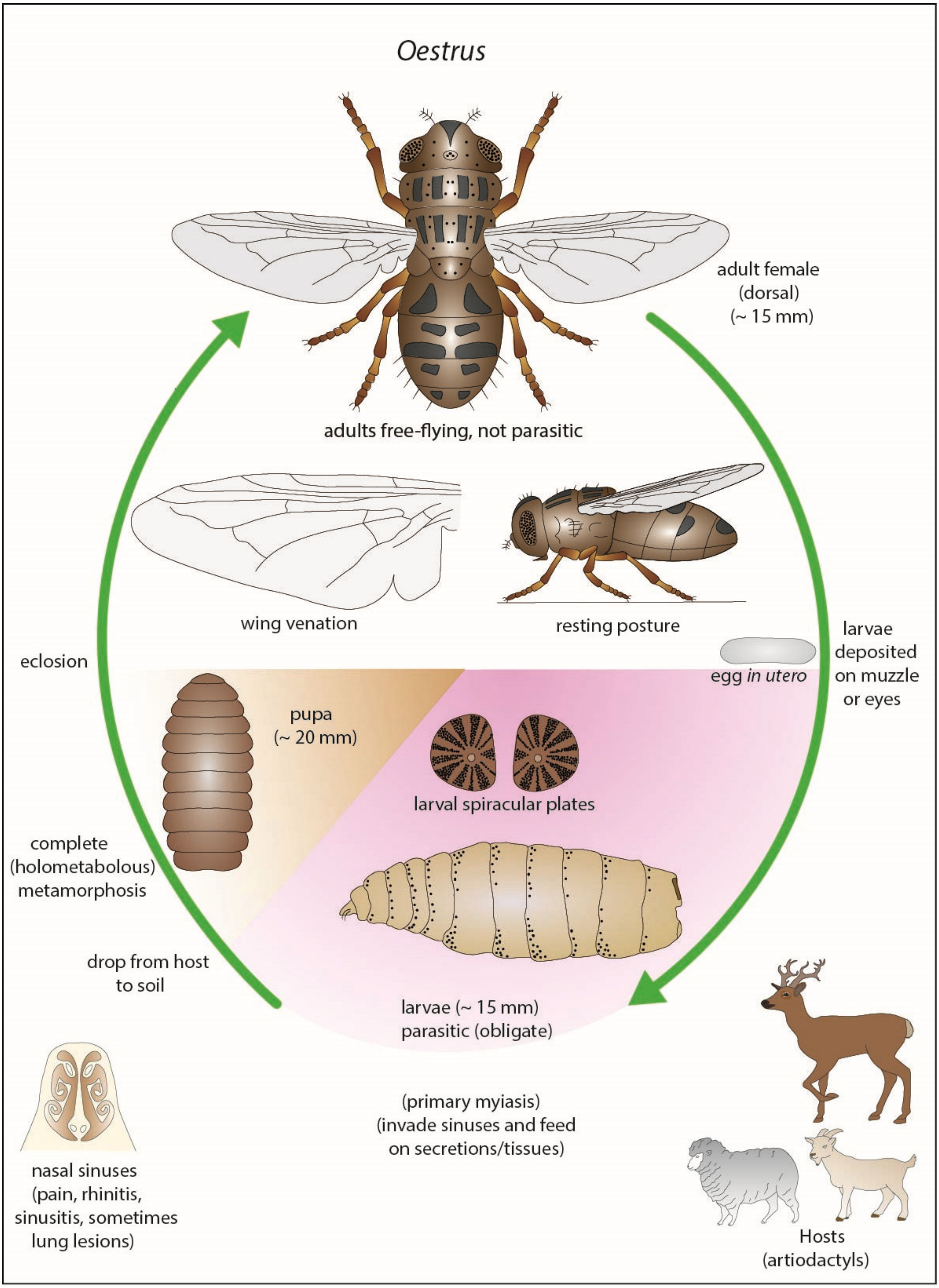
Site of infection: Adult nasal bot flies are not parasitic and they simply do not feed. They are free-flying and gravid females search for suitable hosts on which to deposit larvae, usually by forcibly ejecting packets of larvae onto the muzzle or eyes. The larval stages are obligate parasites and can only complete their development in the upper respiratory passages of a small range of artiodactylan hosts, including domestic livestock (sheep and goats) as well as some wild ungulates (antelope and deer). The larvae exhibit high site specificity (tissue tropism) for the nasopharynx, nasal passages and sinuses, although they may sometimes invade the brain, gums and lungs. Occasionally, first-stage larvae may infest animals and humans in close contact with livestock (such as shepherds and sheep dogs), being found in nasal cavities, frontal sinuses, mouth, pharynx, gums, conjunctival sac, cornea, and ears, but they are unable to develop further.

Pathogenesis: Despite the morbid spectre often associated with nasopharyngeal myiasis, clinical signs are rarely encountered in natural hosts. Sheep often do not exhibit overt signs of infestation, and nasal bot populations generally self-regulate with only around 10 larvae completing development per host. Nonetheless, pathological changes may occur in 4 successive phases: fly worry associated with larviposition; rhinitis caused by first-stage larvae (L1); sinusitis caused by subsequent larvae (L2-3); and lung lesions due to errant larvae. Sheep often react to hovering flies attempting to larviposit and they develop avoidance behaviours to protect their faces from flies, gathering together in tightly-packed groups with their noses dug into the fleece of their neighbours, standing with their heads downcast in clumps of vegetation, or taking refuge in windswept areas. Sheep resume grazing when flies become inactive at dawn and dusk. Over time, sheep may exhibit transient reductions in production parameters due to disturbed grazing and the stress associated with fly worry. Other ungulates (goats, deer) have different browsing/grazing habits and react less to adult flies. Rhinitis develops after larviposition when first-stage larvae (L1) crawl over the mucosa of the nasal passages feeding on mucus and desquamated cells using their mouth hooks and excretory/secretory (ES) products with proteolytic activity. This initially causes a profuse discharge of clear mucus that subsequently becomes mucopurulent and tinged with blood streaks (petechial haemorrhages due to larval mouth hooks and spines). The resultant parasitic rhinitis is characterized by sticky mucoid nasal discharges (sometimes haemorrhagic) with squamous metaplasia and catarrhal inflammation. The volume of nasal discharge is not directly correlated to the intensity of infestation (number of larvae) but appears to be influenced by individual host susceptibility and concomitant infections (worsened by bacterial and/or viral infections). Nasal discharges can become caked with dust in hot dry regions or cause straw, hay and other material to adhere to the nose causing discomfort, distress and breathing difficulties with sneezing, nose rubbing, head shaking, and sometimes stamping of the feet. Affected animals also resort to mouth-breathing which interferes with feeding (grazing and rumination) leading to loss of appetite, emaciation and sometimes death. Sinusitis occurs when larvae enter the frontal sinuses via the ethmoid process and begin feeding on mucus and epithelial cell materials as they grow and develop through another 2 instars (L2-3). Host tissues become inflamed with epithelial changes and copious mucus production. Nasal discharges may persist with a continuation of discomfort, breathing difficulties and altered feeding habits that may impair health and productivity. Clinical signs may also be exacerbated in some individual hosts which develop hypersensitivity responses to larval ES products. When mature, L3 re-enter the nasal passages and exit the host to pupate on the ground. Expulsion generally occurs by bouts of sneezing (often violently) with head shaking and animals seeking support by leaning against structures (trees, posts, walls). Any larvae dying in the sinuses may lead to allergic and inflammatory responses, bacterial infection and septic sinusitis. Lung lesions may also develop when larvae pass down the trachea to lung tissues as well as when purulent discharges are inhaled resulting in lung abscesses and/or interstitial pneumonia. Occasionally, larvae may penetrate the olfactory mucosa and enter the brain causing ataxia, circling and head-pressing. Infestations may also develop in humans and dogs working in close contact with livestock when flies larviposit on them but the larvae usually do not develop beyond L1. Infestations have been associated with transient nasopharyngeal myiasis (larvae in nasal passages, sinuses, pharynx), oral myiasis (mouth, gums) or opthalmomyiasis (conjunctiva and cornea) – the latter being most common and usually manifest as acute conjunctivitis.

Developmental cycle and mode of transmission: These bot flies exhibit holometabolous development in that grub-like larvae undergo complete metamorphosis in pupae transforming into winged adults. Females flies are not oviparous (do not lay eggs) but are viviparous or ovoviviparous (birth live larvae). Eggs are retained within the uterus of female flies where they embryonate and produce first-stage larvae (L1). These larvae are deposited (larviposited) in batches of 3-35 in jets of viscous uterine fluid forcibly ejected from females hovering (often without landing) into the nose or eyes of suitable vertebrate hosts. The larvae are positively thermotactic, negatively phototactic and negatively geotactic and quickly crawl into the nose, mouth, eyes and migrate to the nasal cavities to feed. After several weeks, the larvae migrate to the frontal sinuses or pharyngeal regions where they continue to feed and develop through another 2 instars (L2-3). The time taken for larvae to complete their development is highly variable, and may extend up to 9 months in regions with colder climates. Most oestrid larvae overwinter in their hosts (except the cuterebrines which typically overwinter as diapausing pupae). Mature L3 then return to the nasal passages and are expelled from the host via sneezing (often in energetic bouts). The larvae burrow into the ground (1-10 cm deep) under rocks, stones or vegetation and arch their bodies forming puparia by contraction and hardening of the teguments. The encased pupae develop into an adult over 3-9 weeks depending on environmental conditions (longer in cooler conditions). Adult flies emerge and take flight seeking mates and hosts (for larviposition) using a range of olfactory, visual and thermal cues (plumes of respiratory carbon dioxide, body shapes, colours, temperature and moisture). Male flies gather at aggregation sites (usually prominent hilltops) to intercept passing females for mating. Adult flies do not feed (but may take up water) and they only live for 2-4 weeks. Females may produce 100-600 larvae in their life-times, larvipositing during the hottest part of the day. Flies are most active during hot dry summer months so most infestations are considered seasonal. However, flies may be able to complete 2 generations each year in some subtropical regions.

Differential diagnosis: Nasal bot fly infestations may be suspected on clinical grounds (especially rhinitis/sinusitis, sticky mucus, sneezing) but definitive diagnosis depends on the recovery of larvae for close examination. This is often problematic as the larvae are confined to inaccessible sites (nasal passages and sinuses) for months. Occasionally, larvae may be recovered after severe sneezing attacks, but often they are only detected at necropsy. Examination of clinical parameters may reveal elevated levels of mast cells and eosinophils. Medical imaging technologies may be used to assist diagnoses in individual animals by the detection of soft tissue masses within nasal passages and sinuses. Several immunoserological tests (immunodiffusion, indirect haemagglutination tests and enzyme-linked immunosorbent assays) have been developed to detect specific host antibodies against larval somatic antigens, but they are not broadly available. Molecular biological techniques have also been used to identify and characterize larvae following polymerase chain reaction (PCR) amplification of nuclear (ribosomal DNA) and mitochondrial (cytochrome oxidase I and II) gene sequences.

Treatment and control: Infestations in humans are generally treated by manually or surgically removing larvae where possible, although the larvae do not develop further and die. Supportive therapy is best provided in the form of analgesics, anti-inflammatories, antihistamines and antibiotics to alleviate symptoms and prevent secondary infections. The treatment of livestock is rarely warranted, but clinical infestations are treated using chemical insecticides that may be applied systemically (oral, injectable, sustained-release bolus or pour-ons) so that therapeutic levels may reach the mucosa of nasal passages and sinuses harbouring larvae. Several systemic organophosphates (e.g. trichlorfon) were originally used, but they have now been superseded by salicylanilides (rafoxanide, closantel, nitroxinil) and macrocyclic lactones (ivermectin, doramectin, moxidectin, abamectin) which are highly active against all larval stages. The prevention of infestations revolves around environmental management practices to reduce pupae populations (by seasonally burning pastures and tall grasses) and animal management practices to protect them from questing flies (by stock rotation to pastures beyond the flight range of adult flies). Several attempts have been made to develop vaccines against nasal bot flies. Vaccination with larval extracts and proteins (including serine proteases) did not induce significant protection in sheep, while several salivary gland extracts appeared to be immunogenic. Preliminary studies have also explored several avenues for biological control, involving the release of sterile male flies, and the aerosol application of suspensions of the bacterium *Bacillus thuringiensis* which contain natural insecticides. There are many logistic problems preventing the widespread application of these programs, as larvae cannot be cultured (pupae must be recovered for irradiation), and aerosol sprays must be delivered in confined indoor spaces. At present, no insect repellents have been found to be effective against nasal bot flies.


Oestrus
adult female
(dorsal)
(~ 15 mm)
adults free-flying, not parasitic
wing venation
resting posture
larvae
deposited
on muzzle
or eyes
egg *in utero*
eclosion
pupa
(~ 20 mm)
larval spiracular plates
complete
(holometabolous)
metamorphosis
drop from host
to soil
larvae (~ 15 mm)
parasitic (obligate)
(primary myiasis)
(invade sinuses and feed
on secretions/tissues)
nasal sinuses
(pain, rhinitis,
sinusitis, sometimes
lung lesions)
Hosts
(artiodactyls)

 *Oestrus* adult	 *Oestrus* larva
 *Oestrus* larval spiracles	 *Oestrus* pupa