Stable Fly, *Stomoxys calcitrans* (L.), Dispersal and Governing Factors

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ABSTRACT: Although the movement of stable fly, *Stomoxys calcitrans* (L.), has been studied, its extent and significance has been uncertain. On a local scale (<13 km), fly movement occurs between host animals and resting sites to feed and mate, mainly at on-farm locations where herbivorous livestock regularly congregate. Small numbers emigrate from livestock congregation sites in search of other hosts and oviposition substrate, mostly within <1.6 km. Such local movement occurs by flight ~90 cm above ground, or with moving livestock. While stable flies are active year-round in warm latitudes, cold winters in temperate areas result in substantial population and activity declines, limiting movement of any sort to warmer seasons. Long-distance dispersal (>13 km) is mainly wind-driven by weather fronts that carry stable flies from inland farm areas for up to 225 km to beaches of northwestern Florida and Lake Superior. Stable flies can reproduce for a short time each year in washed-up sea grass, but the beaches are not conducive to establishment. Such movement is passive and does not appear to be advantageous to stable fly's survival. On a regional scale, stable flies exhibit little genetic differentiation, and on the global scale, while there might be more than one "lineage", the species is nevertheless considered to be panmictic. Population expansion across much of the globe likely occurred from the late Pleistocene to the early Holocene in association with the spread of domesticated nomad livestock and particularly with more sedentary, penned livestock.

KEYWORDS: global, host, local, migration, movement, regional, synanthropy, weather

Introduction

Most species of the genus *Stomoxys* (Diptera: Muscidae) are found in Africa and the Palearctic, but the stable fly, *Stomoxys calcitrans* (L.) (Diptera: Muscidae), is the most widely distributed, present in the Western Hemisphere as well as the so-called Old World.[1,2] Stable flies, sometimes called "dog flies", are considered to be a serious economic pest of livestock, being ectoparasites that suck blood from their hosts and occasionally by vectoring various pathogenic organisms.[2–4]

The stable fly resembles the house fly, *Musca domestica* L., and the horn fly, *Haematobia irritans irritans* (L.), 4- to 7-mm long, generally gray with a greenish-yellow sheen, four black stripes on the thorax, the outer two of which are broken, and black blotches or checkering on the abdomen.[1–3] The clear wings are iridescent, and the proboscis is slender, projecting in front of the head.[1,2]

Eggs are deposited in clusters of ~20–100, well within the ovipositional substrate. Ovipositional substrates contain decaying vegetation, excluding dung unless it is comprised of or mixed with vegetation or dropped onto vegetation.[2] The substrate must be moist, and fermentation of the plant matter is particularly conducive for larval development.[3] Examples of substrates in which the pest develops include decaying hay, alfalfa, silage, sugarcane, beached sea grass, lawn cuttings, compost, and piles of waste vegetables.[2,3,5–8] Cattle manure,

however, is sometimes utilized by stable flies for oviposition, particularly on mid-western US cattle feedlots, where high summer temperatures cause exposed manure to dry and develop a crust on the surface, sealing moisture within, thereby creating a relatively long-term, insulated habitat.[2,6] Similarly, buildups of equine manure mixed with straw, particularly around stables, are also important developmental sites, but unaltered deposits of cow, horse, and sheep dung are less conducive.[3] Typically, a female will lay eggs on 4–5 occasions, up to 20 times, and 60–800 eggs can be produced during the life of a female.[1,2]

Eggs hatch in 2–5 days at 26°C, and higher temperatures can reduce that period to ~12 hours.[1,2] Emergent larvae, or maggots, bury themselves in the oviposition substrate to feed and to prevent desiccation.[1] After 12–26 days (12–13 days at 27°C), third instars enter the drier parts of their habitat and pupate.[1,2] Most pupae produce an adult in 5–26 days at 21°C–26°C, and the imago is ready to fly in less than one hour.[1] Adult maximum longevity is variable, from 72 days for females to 94 days for males under laboratory conditions,[1] but longevity is likely <2 weeks under field conditions.[9] Adults begin mating in 3–5 days and females start laying eggs in 5–8 days.[2]

Although stable flies attack a wide range of animals, including rats, guinea pigs, rabbits, monkeys, horses,

humans, camels, goats, and pelicans, cattle are the main hosts.[1,4,10] When the stable fly bites, it quickly draws blood and engorges in 3–4 minutes, which is often interrupted when the fly changes position, and then resumes feeding, often flying from one animal in a herd to another.[1,2] Stable flies mostly feed on the lower parts of a cow's front legs, where shorter hairs present less of an obstacle and where the pest is not likely to be disturbed by the swishing motions of the host's tail.[2] The bites cause pain and annoyance to the afflicted livestock, leading to loss of blood and reduced weight gain and lactation.[11–14] Annual economic costs of weight loss in cattle associated with stable flies and their control were estimated at US$100 million in the US alone.[15] More recently, economic impact of stable flies in the US has been estimated to exceed US$1 billion annually.[16] The average numbers of stable flies per cow range from 25 to 50, but <2 flies per leg was reported to be enough to cause economic loss on feeder heifers.[13,17,18] While stable flies are known to reduce milk production by dairy cattle,[19,20] high-energy feeds can offset that effect.[21]

The stable fly's habit of interrupting its feeding, and moving between host animals, would contribute toward efficiency as a vector of pathogens,[1] which might include *Trypanosoma evansi*, the cause of surra in horses and camels[4,22,23] (but this association is still speculative; it has not been fully demonstrated). Mechanical transmission of the virus responsible for infectious anemia of horses can be accomplished by the stable fly, and West Nile virus was found to be ingested by stable flies feeding on infected American white pelicans, *Pelecanus erythrorhynchos* Gmelin.[10,24] Stable flies are also intermediate hosts for nematode species, *Habronema* spp., occurring in the stomachs of horses, which can also cause skin lesions. There are other diseases linked with stable flies, but most of them are of relatively low importance.[1]

Stable flies are mobile, and their movements have been the source of speculation, suggesting a need for consolidation of existing information. While both short- and long-distance dispersal capabilities are noted for the species, the relationships between them have not been conclusively delineated; rather, they have largely been considered separately. The purpose of this literature-based research is to develop a broader construct on how different modalities and scales of stable fly dispersal contribute toward its establishment on farms and off-farm locations, regional dissemination, and spread across habitable regions of the globe.

Terminology: Movement, Dispersal, Migration

Dispersal is any movement away from an aggregation of individuals or population.[25] Migration is a subset of dispersal, and it is generated by the insect's exertion or by active use of wind or water, and the movement is "persistent", or directed, such that there is little or no turning back to the point of origin while migration is in progress. In this context, migration is not necessarily limited to a preprogrammed movement of

populations between geographic points, as occurs in salmon and monarch butterflies; it can be somewhat less directed such that it would include, for example, the seasonal movement of the convergent lady beetle, *Hippodamia convergens* Guérin-Méneville, to overwintering aggregation sites in mountainous areas.[26] On the other hand, the movement of desert locust, *Schistocerca gregaria* (Forskål), in Africa and Asia depend upon wind and weather fronts, which do not incorporate directed, "persistent", flight, but instead, more passive or opportunistic dispersal reliant on the direction of prevailing weather patterns.[27,28] Desert locust swarms can be moved and deposited on areas that are well suited for continued survival, and to areas that are not, including >1,000 km into the Atlantic Ocean and as far as South America, which was not conducive to establishment.[29]

Flight that has no migratory behavioral component, such as individual movement from one plant or animal host to another, between feeding and roosting sites, and other places frequented by mobile insects, is another subset of dispersal. It generally occurs on a more restricted local scale than migration, or passive or opportunistic dispersal, often involving distances of mere centimeters.

Scales of Dispersal

Local movement. While stable flies are not known to swarm like honey bees, *Apis mellifera* L., or desert locusts by relying on specialized pheromones for that purpose, the pest tends to aggregate at sites frequented by cattle.[30] These sites, however, are fairly specific; stable flies are not randomly distributed. Rather, the pest aggregates where animals stay for regular and relatively extended periods of time, such as loafing sites, holding pens, feeding areas, and milking parlors.[30] To accumulate stable fly populations, a site needs to be used by animals that remain sedentary for at least four hours daily.[31] The numbers of stable flies decline with increasing distances away from those places;[31] hence, local stable fly dispersal patterns and distances traversed are related to animal host distribution and activity patterns rather than wind orientation.[32] While on-farm research has been conducted, stable fly associations with other animals, such as pelicans, camels that are used by nomads, and non-domesticated mammals (sedentary and migratory), are not well understood.

Ingestion of blood from a suitable host is necessary for mating in both sexes and for production of offspring in the female.[33–35] Typically, females ingested bloodmeals an average of 1.8 times per day, and males 2.8 times per day.[36] Females require one or more bloodmeal in order to attain sexual maturity,[37] 3–5 bloodmeals to complete the first ovarian cycle, and three more for additional ovarian cycles.[33,38] Females fed ad libitum on host blood produced >55% and >40% more eggs than females fed only once or twice each day.[39] Close association of the stable fly with its host animals is therefore essential to species survival.

The smallest scale of localized stable fly movement occurs on hosts. At temperatures of <30°C, stable flies are active on the sunny side of the host, but at higher temperatures the flies are more active on shaded parts of the host, or they move to locations near the host that are sheltered from heat.[40] Stable fly movement at cattle congregation sites otherwise occurs between hosts, and males and unmated females fly to the variously termed "resting", "waiting", or "encounter" sites, while mated females move nearer to the oviposition substrate.[40] Another study found that 60% of stable flies collected at resting sites were males, and 26% of the stable flies, regardless of their sex, at resting sites had engorged.[41] Of the females, 37% had not yet fed and up to 54% were unmated.[41] Adults blend with foliage they use as resting substrate, making field aggregations difficult to detect, but they also use man-made structures.[30] Areas where stable flies aggregate tend to include structures such as trees, pole sheds, and barns, on which to alight when not taking a bloodmeal.[31] Males tend to rest on prominent sunlit objects near their hosts throughout the day, peak numbers occurring early in the mornings on cool days, and flight activity is observed mainly during midday hours.[41] Some males rest for several hours, while others have "aerial interactions" with other males.[41] Although males mount females in the air or on the ground, copulation occurs on a perch.[41] During winter between feedings, stable flies mostly bask in the sun at resting sites, maintaining internal temperatures of up to 14.8°C more than ambient temperatures.[41] When the internal temperatures of the flies reach 31–34°C, they move to nearby shaded resting places.[41]

Daily feeding patterns provide an indication of how much movement might occur between the host and resting sites. Each stable fly is reported to feed once per day,[42,43] and several researchers found that daily feeding, determined by numbers of flies on cow legs, was bimodal,[40,44,45] with one morning peak and a larger peak at midday.[43] On cool days, however, unimodal feeding peaks have been recorded[40,43] and comparatively little feeding occurs in the dark of night.[46]

Hogsette et al[30] indicated that stable flies emigrate from host congregation sites in small numbers. Flies travel with cattle as they move about the farm, and many flies are captured along cattle trails.[47] Much of the local movement away from host congregation sites appears to be directed toward other host congregation sites and oviposition substrates, because stable flies orient and settle on warm, moist objects.[30,48,49] Bailey et al[50] found that stable flies are able to travel 3.2 km in search of a bloodmeal, and relatively large stable fly trap catches have been made near sites where straw was used as cattle bedding or stored after such use.[47] This has been corroborated when stable flies were found in nearby suburbs only where fly-contaminated breeding substrates were spread near the homes or within 100 m of on-farm host congregation sites.[47] Local flight occurs across open, cleared areas rather than in wooded areas, hence local travel is mostly conducted along open "corridors", which can result in channeling the flies

to certain areas more than others.[51] Other landscape features might also confine stable fly movement, as demonstrated in a mark–recapture study where marked flies on a lake island remained relatively isolated from mainland populations.[32]

In Thailand, collections of stomoxine flies revealed that, of 10 locations representing four major ecological systems (small local dairy farms, large industrial dairy farms, a national park, and an elephant conservation area), 91.5% were stable flies captured on dairy farms.[52] A time-integrated diffusion model fit to the results of seven sets of experimental results using marked flies indicated that 50% of adult stable flies dispersed >1.6 km from their natal sites on farms, but only 5% dispersed >5.1 km.[53] The most common stage of locally dispersing female stable flies were unfertilized stage 2 nullipars with evidence of a previous bloodmeal,[54] suggesting that movement on a local scale might involve searches for males or other hosts on which to feed to complete the first ovarian cycle and egg fertilization. On the other hand, the percentage of adults with blood remnants in the gut and the percentage of females with yolk increased with greater distances from their site of development, which indicates that survival and dispersal on a local level are associated with prior host finding success.[53] Using flight treadmills, Bailey et al[50] determined that male and female stable flies were capable of flying up to ~29 km but that the average was much less and varied with the age of the fly. It is not likely that measurements taken on flight treadmills represent actual travel under field conditions, which is influenced by many possible factors, including aspects of weather, topography, host distribution and activity, oviposition substrate sites, and diffusion of attractive and repellent volatiles. Local movement by stable flies has been suggested to involve travel of ≤13 km, and whether on- or off-farm, flight occurs at above-ground heights of up to about 90 cm (flight over bodies of water occurs 30–120 cm above the surface).[51,55]

While it is understood that stable flies can be attracted to some colors over others,[30,49,56,57] it is unclear as to the role of color in its local dispersal behaviors. Olfaction is more likely to contribute to local dispersal. Stable flies respond to numerous attractive and repellent volatile agents,[49,57–64] including moist fermenting oviposition substrate.[3]

Springtime populations in regions with relatively cold winters are most likely repopulated from limited local sources of overwintered individuals after most of the flies are extirpated by lethally low temperatures.[65] Survival of immatures is highest at 20–25°C, but mortality markedly increases at ≤15°C.[66] Although some researchers failed to find overwintering populations in farm buildings, including those that were heated,[67] others reported winter breeding in cattle confinement buildings.[65] In temperate New Zealand, a few stable fly adults have been observed during winter, but it is not clear whether they emerged from overwintering pupae or whether they were overwintering as adults.[3] In northern parts of the US, where stable flies overwinter as larvae and pupae, few flies emerged during the winter.[68] Other researchers have indicated

that stable flies overwinter locally and at different life stages, including larvae,[67] despite that being the most vulnerable stage to low temperatures.[66] In south-central Ontario, stable flies move from overwintering farm sites, re-establishing populations on nearby dairy and beef farms in the spring.[69] Movement of stable flies in the spring has been reported to be impaired in flies bearing loads of the phoretic mites *Macrocheles muscaedomesticae* (Scopoli) and *M. subbadius* (Berlese), but the effects of this on stable fly ecology and population dynamics are not understood. In regions with less lethal winter temperatures, adult stable flies are usually observed outdoors on cattle year-round.[69]

In areas of relatively cold winter temperatures, stable fly feeding ceases at <15°C;[46] therefore, most local movement for finding blood meals occurs during the spring, summer, and fall. In higher latitudes, such as Canada, feeding declines as temperatures fall from July through October until it is curtailed during winter.[70] Where temperatures become low, the pest is considered to be a seasonal problem.[56,71] In some temperate and tropical areas, dry weather has been associated with reduced populations, and consequently less feeding activity,[7,43,44,71,72] which can be explained by a reduction in the availability of moist substrates in which larvae develop.

Long-range dispersal. Long distance (>13 km) stable fly dispersal in the field has mostly been reported from northwest Florida beaches and over the Gulf of Mexico when large late summer and fall populations suddenly arrive on northerly winds[30,73] and persist there for about 2 months.[74] Identification of phoretic mite species clinging to stable flies at the northwest Florida beaches revealed that the beach fly populations originate on farms, indicated by the presence of macrochelid mites, well-suited for reproduction in decaying vegetational organic matter such as hay and silage on farms.[74] Jones et al[75] found that similarities among isozyme frequencies were sufficiently strong to indicate that stable flies on the beaches were an intermix of populations originating in agricultural areas north of the beaches; the greatest differences were detected between samples from temporarily isolated populations on the beaches. Flies arriving at the beaches of northwestern Florida are pre- and inter-reproductive stages, most females were nulliparous, and, although on-farm male to female ratios are ~1:1, beach populations were 75% female,[30,55] a finding that has not been explained although food is not likely to be a factor[76] because both sexes require blood-meals and hosts are more available on farms than on beaches.

Hogsette et al[30] suggested that there are two kinds of long-distance dispersal. Type 1 occurs when high-pressure areas in the Midwest or off the Texas coast in the Gulf of Mexico cause northerly winds to blow across northwestern Florida. Stable flies arrive, flying ~90 cm above the ground, on the beaches daily as long as northerlies persist. Type 2 long-distance dispersal involves cold fronts moving across the US and into northwestern Florida, carrying stable flies 30–60 m above ground. This form of transport is largely passive, and the stable flies' final destination is determined by wind direction and the effects of terrain.[30] When the front crosses the land–water interface, the insects are dropped to the ground or to water level by strong downdrafts.[77] After cold fronts pass, the high-pressure area behind the front causes northerlies, creating the conditions for Type 1 long-distance dispersal.[30] As high-pressure areas move eastward and wind strength diminishes, a sea breeze front forms, and during the day, after the land receives sufficient heat from the sun, heated air rises from convection and cool air from the sea moves in to fill the void; the resulting sea breezes direct flies inland, concentrating them in bands.[30] By the following morning, the land is cool, northerlies recommence and return the flies to the beach,[30] explaining the fluctuations in stable fly activity throughout the day.[73] Marked stable flies were determined to have moved up to 225 km from inland locations to the beaches of northwestern Florida within 24 hours.[55] Similar seasonal accumulation of stable flies on the coast of Lake Superior in Michigan[78] suggests that such long-distance movement might also occur elsewhere on prevailing winds.

In a study where ≥10 enzymes in each of 37 separate stable fly populations were examined, extremely low heterozygosity resulted in the inability to use standard genetic identity and distance procedures to determine the divergence of allopatric populations for establishing the source of flies captured on northwestern Florida beaches.[79] Comparing rare alleles in populations grouped from different geographical areas, computing numbers of possible migrants, and analyzing conditional average frequencies of alleles led to the conclusion that stable flies on Florida beaches come from a variety of sites, with agricultural locations northwest of the beaches being the greatest source.[79]

Adults captured in agricultural areas fed more recently than those on the beaches, but in flies that moved ≥60 km, blood-fed individuals were fewer or absent.[75,76] Stable flies have also been reported to feed on nectar, but neither nectar nor aqueous pollen diffusates contribute to reproduction.[76,80] Nectar-fed individuals were more prevalent on beaches than in agricultural areas, indicating that nectar might have a role in long-distance dispersal,[76] although such feeding might also simply be incidental to fewer suitable host animals on the beaches as compared with agricultural areas.

Despite lower quantity of food on the beaches and minimal reproduction compared with farming areas,[79] stable flies can oviposit and develop in bay grasses that have washed ashore.[5,73] The washed-up bay grasses, such as turtlegrass, *Thalassia testudinum* Koenig, and Sims, occur mainly during late summer, but after mid-September deposition of bay grasses along the beaches becomes increasingly infrequent, and eventually ceases.[5,55] On northwestern Florida beaches, adults can emerge 13–18 days after oviposition; in grass that was 7 days old, however, only 50% of eggs lived to adulthood, 14-day-old grass produced <20% adults, and grass aged 21 days reduced adult production to 3%.[5] Because larvae and pupae do not survive winter in washed-up sea grass,[5] it seems

unlikely that this long-distance wind dispersal was a product of evolution. Instead, it was probably incidental to the development of livestock production in inland areas subject to passing weather fronts, which occasionally disperse populations. The relatively large stable fly population displacement to beach areas probably did not occur until it was facilitated by human-induced livestock production inland.

Large-scale dispersal.

Regional. Starch gel electrophoresis analysis revealed limited gene flow and genetic diversification among nine populations of stable flies in Thailand.[80] Although polymorphism varied among regions,[81] no correlation was detected between genetic diversification and geographic distance.[81,82] Electrophoresis of 10 isozymes showed a corroborating degree of genetic homogeneity on a countrywide scale in Thailand,[81] and stable flies across North America have been reported as showing little genetic differentiation.[59]

Stable flies, having presumably evolved before humans kept livestock, were probably associated with watering holes, wallows, and thickets where wild herbivores congregated. Before humans domesticated herbivores, stable fly dispersal was likely facilitated on a regular basis by weather fronts and by wildlife migrations and displacements. Weather front dispersal, apparently being unrelated to the odds of establishment where the flies are eventually deposited, might have been responsible for limited expansion on a regional scale. Wildlife migrations tend to be seasonal, and involve areas confined to the destinations and places along the route, but they would not push the range of the host, and that of the stable fly, farther. Human domestication of animals provided a more deliberate, and ultimately wide-ranging and accelerated, mode of regional dispersal. Ice ages might have influenced the extent to which stable flies dispersed on a regional scale by changing wildlife migration patterns and human expansion, and by causing temperature reductions below the range favored by stable flies. Because reproduction occurs between 20 and 30°C,[83] establishment of populations is limited to latitudes and elevations with relatively moderate temperatures.[66,83] It was probably the stable fly's synanthropic association with livestock herded by nomads, in many instances camping at watering holes already harboring stable flies, that spread stable flies most efficiently from region to region. Where humans began settling and containing their livestock and pack animals in pens and pastures, the accompanying stable fly population likely increased in response to a relatively profligate availability of hosts and reproductive habitat. Hot, dry regions are also not habituated by stable flies (upper range is 35°C, to which pupae are the most vulnerable),[66,84] and dry regions are unsuitable for stable flies because development as larvae requires moist substrate.

Global. In the absence of a fossil record of stable fly distribution and host preferences, it is not possible to extrapolate suppositions with certainty to eras before the advent of humans and the domestication and movement of livestock. If stable flies at one time fed on dinosaurs, for example, we do not have that information. However, our understanding about stable flies and their hosts offer some hints as to various ways in which the insect might have survived, but not necessarily exactly how it moved from one place to the next. In addition to living at watering holes and wallows supporting large herbivorous mammals, it is possible that relatively small stable fly populations also existed around rodent colonies, and even rookeries of some avian species.

Endo- and ectoparasitic arthropods of veterinary importance were most likely introduced, barring certain weather events, to new areas with their domesticated herbivorous hosts.[85,86] Using mitochondrial DNA (COI 550 bp) and r16S DNA (300 bp), Marquez et al[86] determined that, at a minimum, New World stable flies had Palearctic origins within the past 500 years. Dsouli et al[84] examined five major zoogeographic regions to analyze stable fly population's genetic structure and to trace its global dispersion. Mitochondrial (COI, Cyt-b, and ND1-165) and nuclear (ITS2) DNA showed a substantial differentiation of Oriental populations (referred to as "first lineage") from the Afrotropical, Palearctic, Nearctic, Neotropical, and Oceanian populations (second lineage).[84] Findings suggest separation between the two lineages during the mid-Pleistocene; Oriental populations were isolated and unlikely to have been involved in the colonization of other regions.[84] Demographic analyses indicate that Oriental, Afrotropical, and Palearctic regions have undergone a population expansion from the late Pleistocene to the early Holocene,[84] when global human dispersal occurred.[87,88] High levels of gene flow among Nearctic, Neotropical, Palearctic, and Australian biogeographic regions suggest that population expansion, and the majority of genetic diversity, occurs within groups, and much less so between groups.[89] Stable fly genetics have, as a result, been characterized as being panmictic, with no isolation by distance or across geographical barriers.[89] As with regional dispersal, global dispersal appears to be most limited by temperature- and moisture-related barriers relating to latitudes, elevations, and deserts.

Conclusions

Stable fly dispersal occurs, and has occurred, at different scales, from local to global, and synanthropy is integral to each. Local movement occurs chiefly between hosts, to resting areas and oviposition substrate, and with local movements of livestock and pack animals. Terrain, weather, and host and habitat dispersion are involved in short-range dispersal of <13 km, but congregation of hosts with oviposition substrate are needed for population establishment. Human-facilitated aggregation of livestock and pack animals, especially in holding areas, increases stable fly populations, which contributes toward greater sum local movement, and probably the likelihood of emigration from one host congregation site to another whether by direct flight or by accompanying host animals in transit.

Dispersal at the regional scale likely occurred to some extent before the rise of humans and domestication of livestock

and pack animals. Weather fronts might have moved stable flies from limited (eg, watering hole) populations of wildlife to new areas, but because of the passive nature of this kind of dispersal, establishment in new regions was probably the result of downdrafts occurring at interfaces between land and large bodies of water. In the instances reported, northwestern Florida beaches and a shoreline of Lake Superior, deposition of stable flies does not necessarily mean they will become established if the new area or region is unfavorable to development and reproduction. Wildlife migrations and the propensity of herbivorous animals for water holes were likely greater factors in regional dispersal. Stable fly populations and distribution probably increased substantially as humans began keeping livestock and pack animals, and this likely accelerated when humans maintained domestic herbivores within enclosures where both host and development substrate resources were stabilized, magnified locally, and multiplied geographically between regions, and as a result, globally.

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Author Contributions

Conceived and designed the experiments: ATS. Analyzed the data: ATS. Wrote the first draft of the manuscript: ATS. Contributed to the writing of the manuscript: ATS and WLAO. Agree with the manuscript results and conclusions: ATS and WLAO. Jointly developed the structure and arguments for the paper: ATS. Made critical revisions and approved the final version: ATS and WLAO. Both authors reviewed and approved of the final manuscript.

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