Biology of Subterranean Termites in the Eastern United States

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Subterranean termites are social insects that live in societies whose members are mostly immature individuals. Their colonies, which can contain thousands to millions of termites, are formidable, even though each individual termite is soft-bodied and delicate. In nature, subterranean termites are closely associated with the soil habitat where they tunnel to locate water and food (e.g., wood, fallen logs, and other cellulose-containing materials). Termites excavate galleries throughout their food as they consume it. They conceal their workings and can completely honeycomb wood by feeding along the grain and following the softer spring wood, leaving little more than a thin wooden exterior (**Fig. 1**). Subterranean termites construct aboveground earthen runways (shelter tubes [**Fig. 2**]) that protect them from the drying effects of air as well as from natural enemies, such as ants. Termites are very susceptible to desiccation, and thus they are dependent on moisture sources.

Figure 1. Subterranean termites excavate galleries in wood as they consume it, sometimes leaving nothing more than a thin wooden exterior.
(B.T. Forschler)

Figure 2. Termites build shelter tubes to protect them from the drying effects of air and from natural enemies, such as ants.
(B.T. Forschler)

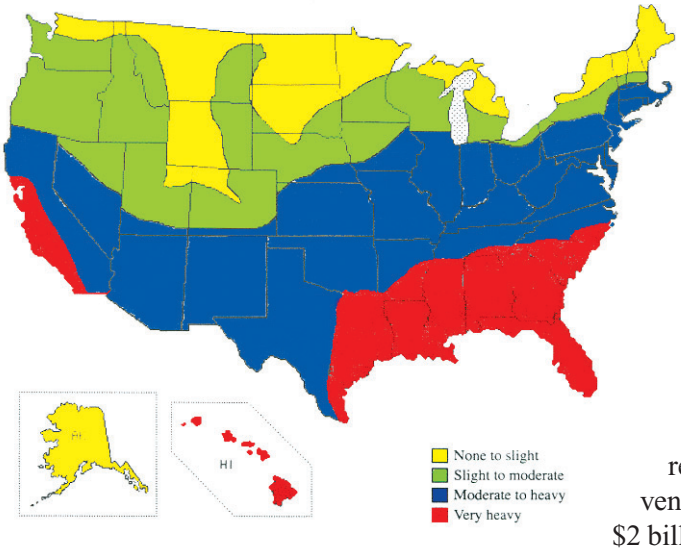


Figure 3. Subterranean termites are found in all states except Alaska and are most abundant in the south and southeastern United States.

Distribution and Economic Impact

In the United States, subterranean termites are found in every state except Alaska. They are most abundant in warmer climates, where structural infestations are common (**Fig. 3**).

Subterranean termites are the most economically important wood-destroying pests in the United States. They are, however, important components of natural forest ecosystems, where they break down cellulose. Unfortunately, when land is cleared for human habitation the termites present may eventually pose a threat to the wood used in construction because their natural food resources have been removed. Nationwide, treatment and prevention of subterranean termite infestations costs approximately $2 billion per year. In Georgia alone, residents spend over $200–300 million per year for the remedial control of existing infestations and the repair of damage that subterranean termites cause to homes and other structures.

Types of Subterranean Termites

Native Subterranean Termites

Most subterranean termite species that occur in the eastern United States are native to North America. For example, the **eastern subterranean termite**, *Reticulitermes flavipes* (Kollar), is the most widely distributed subterranean termite, and it is the most common termite found in the eastern United States. Due to its widespread distribution, *R. flavipes* is likely the most economically important termite in the United States. The **dark southeastern subterranean termite**, *Reticulitermes virginicus* Banks, and the **light southeastern subterranean termite**, *Reticulitermes hageni* Banks, are generally less economically important when compared to *R. flavipes* because they are not as widely distributed.

Introduced Subterranean Termite

The **Formosan subterranean termite**, *Coptotermes formosanus* Shiraki, was accidentally introduced into a number of port cities in the southern and southeastern United States shortly after World War II. To date, the distribution of the Formosan subterranean termite is patchy. It has been reported from various cities in Alabama, California, Florida, Georgia, Hawaii, Louisiana, Mississippi, North Carolina, South Carolina, Tennessee, and Texas. The Formosan subterranean termite is spread via human commerce, especially in used railroad crossties incorporated into landscapes. Formosan subterranean termite colonies are, on average, larger than colonies of native *Reticulitermes* subterranean termites.

Subterranean Termite Biology

Social Insects

Termites, like other social insects, are characterized by:

- cooperation in the rearing of young,
- sharing of resources (i.e., food, water and shelter),
- an overlapping of generations (i.e., eggs are laid year-round), and
- a division of labor, characterized by the presence of one or more castes, or life forms.

Figure 4. Worker termites with one queen and three kings. (S. Grube)

Termites are insects that live in loosely associated societies called colonies. A colony is a collection of individuals that cooperate in the rearing of young and that share resources (e.g., food and shelter). Some scientists view the termite colony not as a collection of individuals but as a single living entity whose parts (i.e., individual termites) work together towards the survival and reproduction of the whole (i.e., the colony). Termite colonies are comprised of a few adults (the king and queen) while the majority of the population are immature forms that are represented by approximately equal numbers of males and females (**Fig. 4**).

Colony structure in subterranean termites likely does not reflect the model of other insect social organizations. In general, most social insects have a colony structure where the majority of members are females concentrated in a single, centralized, immobile nest from which workers forage in search of food and water. Subterranean termite social groups are composed of both males and females and have a mobile nest site usually located near food, most often some form of dead wood that they excavate and inhabit.

Figure 5. Worker termites are the most numerous caste and are responsible for the damage to wood. (B.T. Forschler)

Termite Castes

Termites exhibit a caste system of organization, wherein physically distinct individuals perform different tasks in the highly structured termite society. The proportion of each caste is regulated by a variety of environmental factors as well as the presence or absence of caste-regulating pheromones (chemicals) produced by the termites themselves. Generally, three castes are recognized:

- the worker caste,
- the soldier caste, and
- the reproductive caste.

The Worker Caste

Worker termites (**Fig. 5**) are physically and sexually immature males and females and are the most numerous caste. These wingless, white insects are typically the first termites seen when an active shelter tube, infested log, or piece of infested structural wood is breached. Workers are blind and probably only perceive changes in light intensity.

Figure 6. The soldier caste's primary function is colony defense. (S. Grube)

Figure 7. The alate caste is responsible for starting new colonies. (D. Shetlar)

Figure 8. Shed wings on a window sill are a sign of infestation. (B.T. Forschler)

Workers destroy wood because they consume it. They are called workers because they perform most of the labor associated with colony maintenance. Worker termites are involved in numerous tasks such as locating and colonizing food resources; excavating, repairing, and building galleries and shelter tubes; feeding, grooming, and caring for young termites, reproductives, and soldiers; and participating in colony defense.

The Soldier Caste

Soldier termites (**Fig. 6**) are physically and sexually immature males and females whose primary function is colony defense. Soldiers are easily identified by their enlarged, yellowish to yellowish-brown head and long, hard black mandibles (mouthparts) that they use to ward off enemies, primarily ants and termites from other colonies. Soldier termites are wingless, blind, and otherwise soft-bodied.

In *Reticulitermes*, soldiers typically comprise 1–2% of the termites present in a colony, whereas Formosan subterranean termite soldiers comprise 10–15% of the population. Because soldiers are not capable of feeding themselves, workers provide them with regurgitated food.

The Reproductive Caste

Adult winged termites, called **alates** or swarmers (**Fig. 7**), have two pairs of long, narrow wings of equal size, thus describing the name of the Order of classification to which termites belong—Isoptera; *iso*, meaning equal, and *ptera*, meaning wing. Alate termites have fully functional wings and eyes, and their pigmented, dark skin can better tolerate water loss than the aforementioned immature forms. Unfortunately, alate termites are sometimes mistaken for flying (alate) ants. A winged termite can be easily distinguished from a winged ant by the following characteristics (**Refer to foldout**):

- the presence of straight to slightly curved, beaded antennae (winged ants have distinctly elbowed antennae),
- the lack of a "waist" (winged ants have a distinct constriction between body regions), and
- the presence of two pairs of equal size wings (winged ants have two pairs of wings, but the front pair is larger than the hind pair).

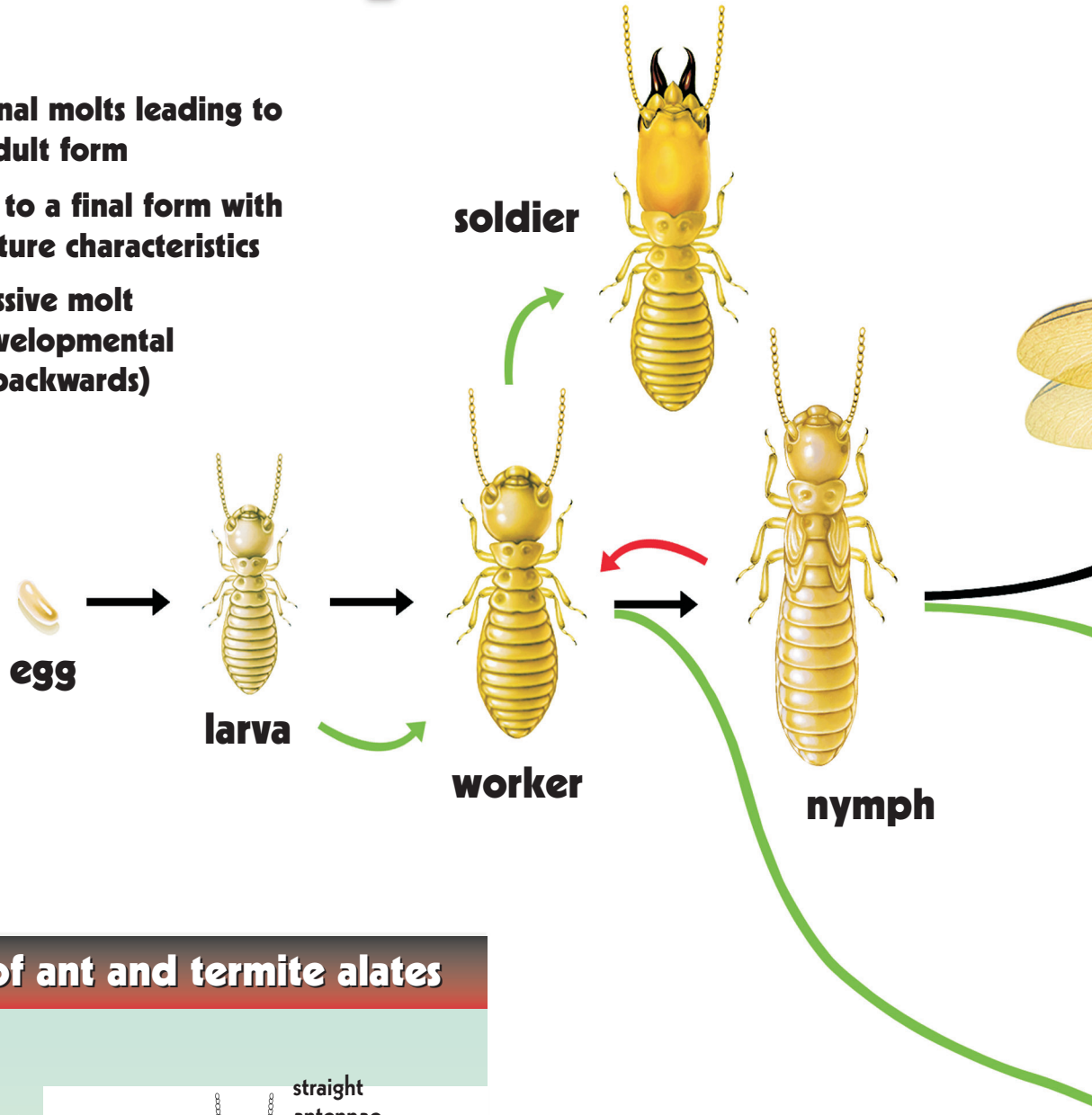
The sudden, dramatic appearance of alate termites is commonly referred to as *swarming*, and when it occurs indoors is often one of the first signs of a structural infestation (**Fig. 8**). Subterranean termites swarm in an attempt to initiate new colonies. Fortunately for homeowners the success rate of colony establishment via swarming is extremely low because most alates die soon after swarming. Alates commonly succumb to desiccation, predation, and other environmental factors. Swarming occurs mainly when outdoor temperatures are warm, and usually only by mature colonies. In warm sections of infested structures termites may swarm during the winter, although this is not common.

Subterranean Termite Life Cycle

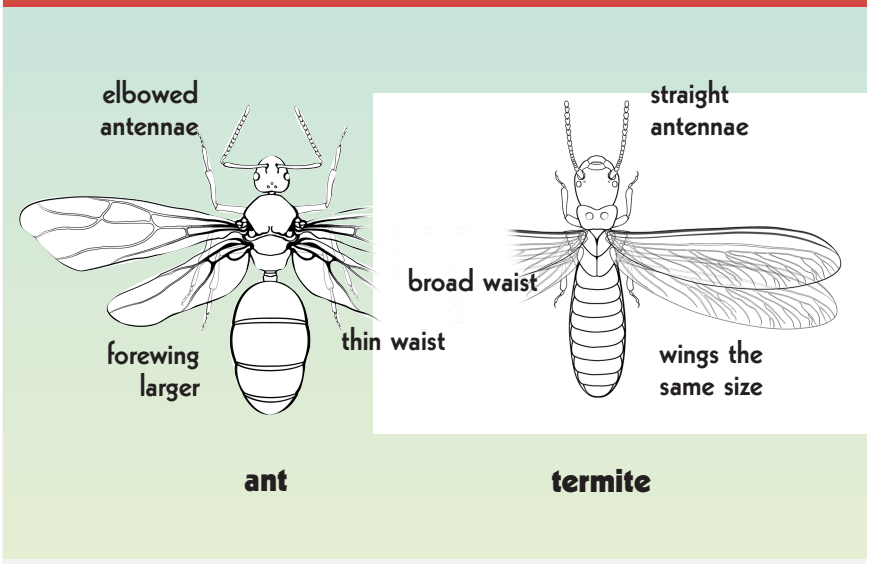
black lines – imaginal molts leading to the adult form

green lines – molts to a final form with immature characteristics

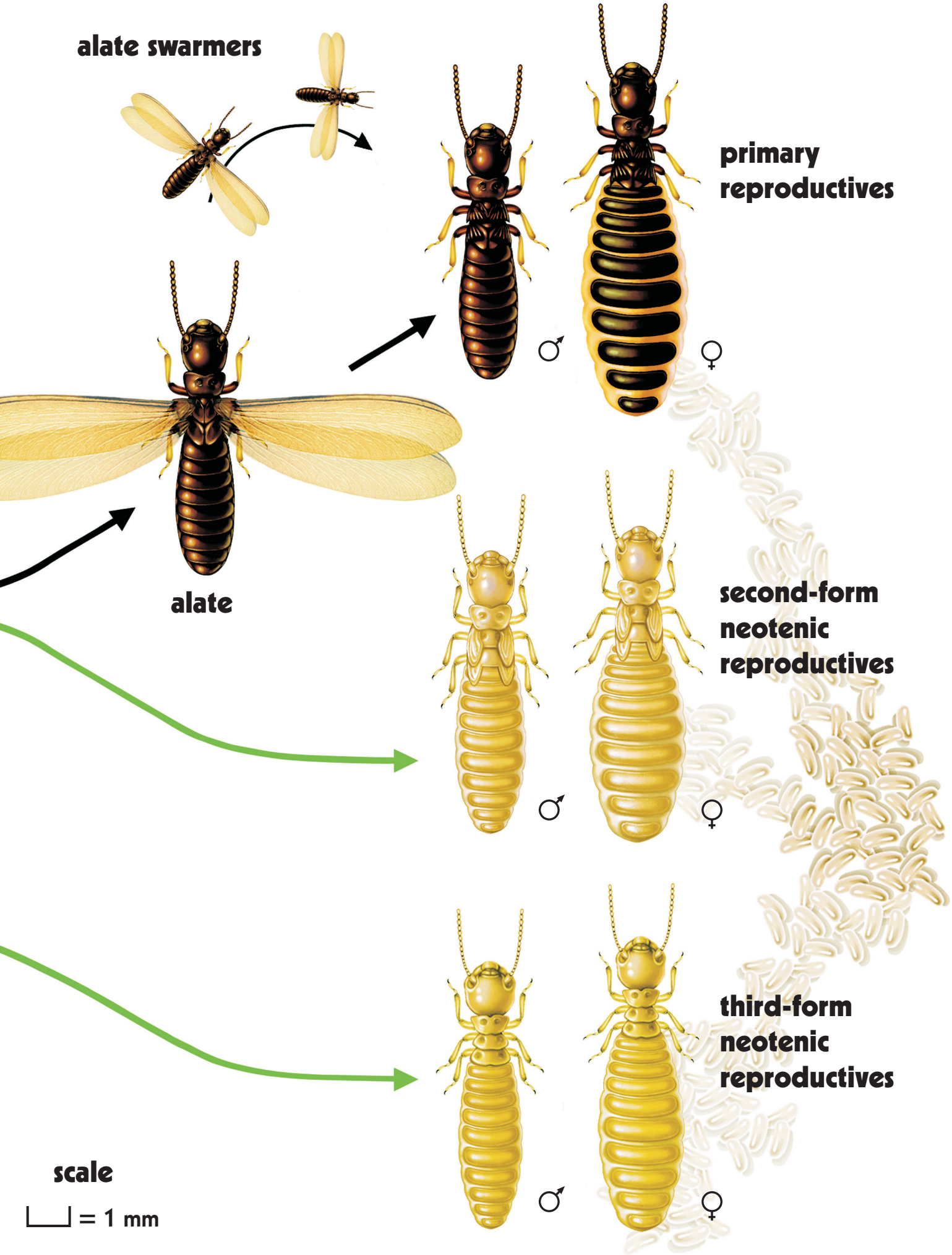
red line – regressive molt (a developmental step backwards)



Comparison of ant and termite alates



Illustrations by Erin Daniels


alate swarmers
alate
primary reproductives
second-form neotenic reproductives
third-form neotenic reproductives
scale
= 1 mm

The eastern subterranean termite typically swarms from February through April, while the dark southeastern subterranean termite swarms from April through June. Alates of both species are brownish black to black. The light southeastern subterranean termite typically swarms from July through September. The light southeastern subterranean termite gets its name from the yellowish brown body of the alates. Native subterranean termites swarm during the day, while the Formosan subterranean termite swarms from dusk until about midnight from April through July. Formosan subterranean termite alates are yellowish brown, and their wings are covered with very fine hairs. Formosan subterranean termite alates are considerably larger than the alates of native subterranean termites found in the eastern United States.

Soon after swarming, male and female alates lose their wings and form pairs. A pair that successfully establishes a new colony is called the **king** (male) and **queen** (female) of the colony (**Fig. 9**); they are also referred to as the **primary (first form) reproductives** because they have attained the adult stage and are physically and sexually mature. Within the first few days or weeks after pairing, the queen lays the first clutch of several dozen eggs; small numbers of eggs are laid intermittently thereafter. The king and queen take care of the first batch(es) of eggs and young. When a number of workers are present, they begin caring for their younger nestmates, eggs, and the primary reproductives. Initial colony growth is slow, but as the queen ages her egg-laying capacity increases and colony growth rate accelerates (**Fig. 10**).

Under certain conditions and circumstances, some immature male and female termites mature sexually and become **neotenic reproductives** (**Fig. 11**). Unlike primary reproductives, neotenic reproductives do not develop wings, compound eyes, or uniformly pigmented skin. Neotenic reproductives enhance colony egg production, and thus colony growth. Numerous neotenics can contribute to overall egg production in a colony, hence exceeding, many times over, the egg production of a single primary reproductive. The number of neotenic reproductives in a colony in no small part determines how fast a colony will grow and the size it may eventually attain.

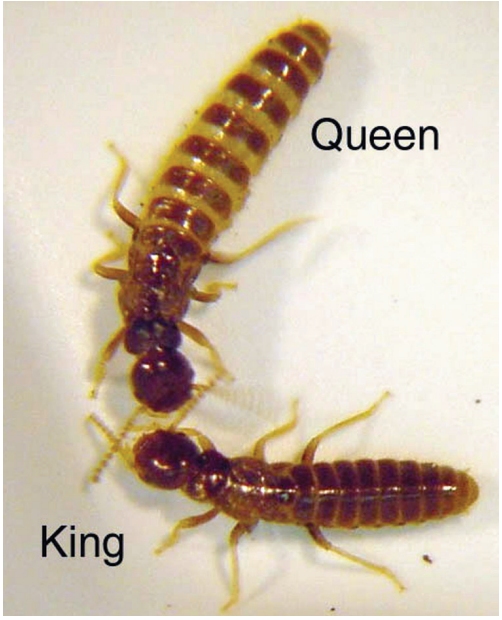


Figure 9. Primary reproductives. (S. Grube)

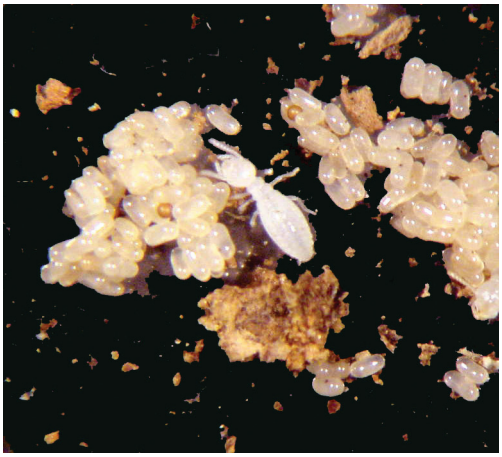


Figure 10. A cluster of eggs with a larval termite. (S. Grube)

Figure 11. Female neotenic reproductives. (S. Grube)

The Termite Life Cycle

Termites are opportunistic—a trait most aptly demonstrated by the variety of developmental options available to this small, delicate social insect. The ultimate caste, or life form, of an immature termite is not determined at the egg stage. Each newly hatched termite can develop into any one of a number of castes. These complexities are highlighted by the subterranean termite life cycle (**Refer to foldout**). As illustrated in this fold-out diagram, a **worker** can remain a worker for its entire life span (estimated range from 1–4 years) as it undergoes numerous molts (sheds its skin) without changing into another caste. Alternatively, a worker can molt twice, where it first becomes a **pre-soldier**, then subsequently a **soldier**. The soldier caste can no longer molt and is considered a terminal (final) stage.

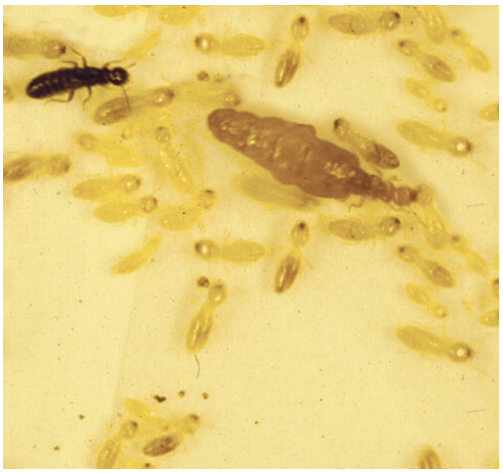


Figure 12. A male primary and female neotenic reproductive. (B.T. Forschler)

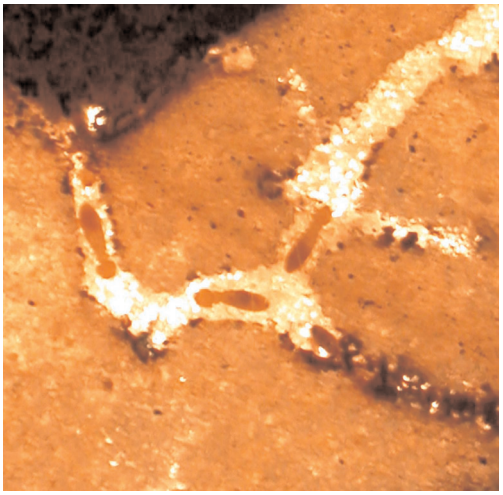


Figure 13. Termites forage following gradients and physical guidelines. (B.T. Forschler)

Worker termites can also develop into winged, adult termites (alates), but they must first pass through an intermediate stage called the nymphal stage. **Nymphs** are termites with external wing buds. Large numbers of nymphs are produced on a seasonal basis, usually starting in late summer. As nymphs progress toward the adult stage (i.e., alate) they molt several times, typically over the course of several months, to fully develop wings, eyes, and functional reproductive organs. Nymphs can ultimately molt into sexually mature, fully winged adult male or female **alates**.

Nymphal termites are also capable of a unique developmental pathway wherein they sometimes undergo a regressive molt and lose their wing buds, thereby reverting back to the worker stage. These workers are called **pseudergates**.

A colony may contain several types of neotenic reproductives. **Secondary (second form) reproductives** develop from nymphs, and are therefore characterized by the presence of small wing buds. **Tertiary (third form) reproductives** develop from workers and hence lack wing buds.

The developmental flexibility of termites plays a key role in their ability to disperse and establish new, functional colonies when infested materials are transported to new locations. Additionally, neotenic reproductives may develop functional colonies inside buildings, but only if adequate moisture is available inside the structure.

Reproductives and Colony Composition

Recent research indicates that subterranean termite social structure is dynamic (**Figs. 4, 9, 11, 12**). The latest evidence suggests that termite colonies form and separate based on available resources, environmental conditions, and the relatedness of nearby groups of termites. There is an emerging view that termite colonies can be composed of the offspring from a single adult queen or from several adult queens (and an undetermined number of kings) (**Fig. 4**). The composition of the reproductive structure of a termite colony can range from an association formed around a single primary queen to any number of queens and/or neotenic reproductives.

Foraging Behavior

All termite castes are mobile throughout their life. Even reproductives freely move from one feeding site to another. As a result of this mobility, there appears to be no permanent central nest area. On any given day reproductives, eggs and/or very young termites might be found in the different sites occupied by a colony. Termites living within their food resource are free to move from one location to another within the network of galleries inside and connecting the various food resources identified by their nestmates. The colony is thought to concentrate its activity in different locations at different times. Termite activity might be concentrated in one section of their feeding range at one point and just days or weeks later might shift to yet another section.

When searching for food, termites follow chemical and moisture gradients in the soil, as well as physical guidelines such as roots, abandoned insect and earthworm tunnels, foundation elements, and cracks or crevices in the soil profile (**Fig. 13**). Termite foraging activity in soil usually is confined to areas of adequate moisture and moderate temperature.

What Subterranean Termites Need to Survive: Food, Water, and Warmth

Food of subterranean termites consists of anything made of or containing cellulose. Termites feed primarily on dead wood and wood by-products, and only under unusual circumstances will they feed on other living or dead plant tissue. However, in their search for food, termites can tunnel into and damage a variety of noncellulose materials (e.g., rigid foam-board insulation, sheetrock, etc.) (**Figs. 14–16**).

Termites prefer to feed on soft, spring growth wood rather than hardwoods and woods rich in natural chemical protectants. Some woods (e.g., redwood, cypress, juniper) are less preferred by termites, but no wood is completely immune to attack. In general, termites prefer cellulose that is easy to obtain. For example, in laboratory studies, they prefer in this order: loose cellulose fibers > paper > cardboard > softwood blocks > hardwood blocks. In the field, preference for a particular cellulose resource is likely determined by its availability, size, texture, and the nutritional demands of the termite colony. As termites break off wood fibers, they swallow the small fibers, which then undergo complete digestion by protozoans, bacteria, and enzymes in the termite hindgut.

The association of termites and fungi is quite complex. There is some evidence that termites prefer wood that has been attacked by certain wood-destroying fungi. Other fungi may deter termite feeding. Wood-destroying fungi often take advantage of the same moist conditions favored by termites. Thus, termites and wood-destroying fungi are sometimes found together in structural infestations.

Moisture is the most important factor limiting subterranean termite activity and distribution in the environment. Termites are thin-skinned insects that quickly dry out when exposed to the desiccating effects of wind or dry air and they require a constant supply of moisture. In suburban areas where irrigation occurs regularly, and soil moisture is not limited, colonies are thought to be more active.

The gallery system that termites excavate within soil and wood allows for near complete saturation of the air inside. The wood and the soil act like a sponge, holding onto the water and helping to maintain a high humidity in areas where the termites live and feed. Such high humidity helps minimize cuticular (skin) water loss. Subterranean termites can transport moisture and soil to aboveground feeding sites. In exposed areas, termites travel within shelter tubes (**Fig. 2**). Shelter tubes are constructed by termite workers and are composed of particles of soil, wood, and other debris held together with glue-like saliva and other secretions.

Figure 14. An example of foam-board insulation riddled with termite galleries. (B.T. Forschler)

Figure 15. A fallen apple damaged by subterranean termite feeding. (B.T. Forschler)

Figure 16. Warm, moist wood provides subterranean termites with all of their survival requirements. (B.T. Forschler)

Figure 17. The siding was removed from the porch and an exterior wall of this house to show the extent of termite damage. (B.T. Forschler)

Figure 18. An example of the natural habitat of subterranean termites. (B.T. Forschler)

Although rather uncommon, subterranean termites can survive and form functional colonies in aboveground locations without maintaining contact with the soil if sufficient moisture is available. Sources of moisture include water pooled on the roof, water trapped behind the external siding or veneer of buildings, water in stopped-up gutters, and water resulting from leaky plumbing or air conditioning units.

Temperature has a strong influence on daily and seasonal fluctuations in termite activity. Subterranean termites will not forage for food when topsoil temperatures are either too hot or too cold. They adjust their activity to seek suitable temperatures and will migrate deeper in the soil when surface temperatures are unsuitable. Foraging termites can also detect temperature gradients in the soil, and under extremely hot conditions seek out thermal "shadows" cast by vegetation, and presumably structures. When temperatures near the soil surface are too hot and the soil becomes dry, termite foraging may be significantly reduced.

In climates where winter temperatures are extremely cold, termite foraging is limited due to nearly frozen or frozen topsoil. Little is known about termite foraging behavior during the winter. Termites most likely remain active in cold weather if the structure they are infesting is heated.

Summary

Subterranean termites are the most economically important wood destroying pests in the United States. Nationwide, billions of dollars are spent annually to control subterranean termites and to repair the damage they cause (**Fig. 17**). However, in nature, subterranean termites are important components of forest ecosystems, where they break down dead cellulose into its basic elements for use by plants and animals (**Fig. 18**).

Only recently have scientists begun to unravel many of the biological complexities of these cryptic subterranean insects. We are only now becoming more aware of the opportunistic nature of subterranean termites and the plasticity of their life cycle, colony structure, and foraging behavior. The developmental flexibility of termites enhances their ability to disperse and to establish new colonies. Knowledge of termite biology ultimately provides a firm foundation for understanding control measures and for developing new termite control technologies.

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