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Biology, Behavior, and Ecology of Stored Fruit and Nut Insects

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Tree nuts and dried fruits vary widely in their quality as hosts for insect pests, but stored product pests can cause economic loss even in commodities that are generally poor hosts. Economic damage can be due to commodity consumed, but the very presence of insect body parts, frass, or webbing can cause expensive rejections and loss of market at the wholesale level due to quality concerns or phytosanitary regulation. Most USDA quality standards for dried fruits and nuts do not allow for any live insects (USDA-AMS 2011).

Stored product pests of dried fruits and nuts can be divided (with some qualifications) into two categories: orchard pests that primarily infest the orchard and do not reproduce in storage, yet affect marketability; and pests that infest and reproduce in storage. In this chapter, the biology of selected pests of dried fruits and nuts in storage are presented. Species descriptions are presented in three groups (Table 1). The first group includes three moths — the codling moth, navel orangeworm, and the carob moth — which are predominantly field pests that infest the marketable fruit or nut. The second group includes non-lepidopteran pests, the driedfruit beetle and vinegar flies, which infest predominantly in the field. Unlike the moth pests, the driedfruit beetle and the vinegar flies feed as adults. The third group includes the Indianmeal moth, almond moth, tobacco moth, and the raisin moth. These last four moths are predominantly storage pests. They (and the Mediterranean flour moth, Chapter 4) respond to the same principal pheromone component, and might be found in the same pheromone trap. Except for the

codling moth, each of the moths in this chapter is of the subfamily Phycitinae (Heinrich 1956, Solis 2011).

In addition to these species, the red flour beetle, *Tribolium castaneum*, and the sawtoothed grain beetle, *Oryzaephilus surinamensis*, as well as a variety of other beetle species (Simmons and Nelson 1975), also infest and reproduce in dried fruits and nuts during processing and storage. Their biology is described in Chapter 4. Common names are used here are in accordance with the Entomological Society of America (ESA 2011), but these vary widely internationally, even within the English language.

Life Histories



Figure 1. Codling moth adult and larva (Jack Kelley Clark, courtesy University of California Statewide IPM Program).

Codling moth *Cydia pomonella* (L.)

Adults are mottled gray with brown wing tips, slightly under 0.5 inch long, with wings covering the top and side of the body. Adults do not feed.

Table 1. Hosts and geographical distribution of selected insect pests of dried fruits and nuts

Species	Reproduces in storage?	Hosts	Geographical range	References
Codling moth <i>Cydia pomonella</i>	No	Pome fruits, walnuts	Cosmopolitan	(2)
Navel orangeworm <i>Amyelois transitella</i>	No	Walnuts, almonds, pistachios, figs	Tropical and subtropical Western Hemisphere	(7; 10; 15; 17)
Carob moth <i>Ectomyelois ceratoniae</i>	Yes	Dates, figs, almonds, pomegranates, and citrus	Nearly cosmopolitan	(4; 7; 12-14; 17)
Driedfruit beetle <i>Carpophilus hemipterus</i>	No	Figs, raisins, dates	Cosmopolitan	(4; 7; 8)
Vinegar fly <i>Drosophila</i> spp.	Maybe	Figs, raisins	Cosmopolitan	(16)
Indianmeal moth <i>Plodia interpunctella</i>	Yes	Wide range of stored products	Cosmopolitan	(7; 11; 17)
Almond moth <i>Cadra cautella</i>	Yes	Wide range of stored products	Cosmopolitan	(5; 7; 17)
Tobacco moth <i>Ephestia elutella</i>	Yes	Dried fruits, nuts, grain and cereal, chocolate, cocoa, and tobacco	Nearly cosmopolitan	(1; 3; 6; 7; 17)
Raisin moth <i>Ephestia figulilella</i>	No	Dried fruits, nuts, seeds, beans	Nearly cosmopolitan	(5-7; 9; 17)

References cited: 1) Ashworth 1993. 2) Barnes 1991. 3) Bell 1975. 4) Blumberg 2008. 5) Cox 1975b. 6) Donohoe et al. 1949. 7) Heinrich 1956. 8) James and Vogele 2000. 9) Kehat et al. 1992. 10) Legner and Silveira-Guido 1983. 11) Mohandass et al. 2007. 12) Mozaffarian et al. 2007. 13) Navarro et al. 1986. 14) Nay and Perring 2006. 15) Plant Health Australia 2009. 16) Simmons and Nelson 1975. 17) Solis 2011.

The codling moth is oligophagous (i.e., limited to a few hosts); larvae develop principally on fruit from the family Rosaceae, and on walnuts (Barnes 1991). Flat, oval eggs are laid singly on nuts or on leaves near nuts. Larvae enter soft, immature nuts quickly, but may require a week to enter hardened walnuts (Barnes 1991). Codling moth larvae are white to tan with a dark head capsule and prothoracic shield, and they lack the sickle-shaped prothoracic spiracle characteristic of navel orangeworm and carob moth larvae. Codling moth larvae exit fruit or nuts to pupate.

Codling moth survives the winter in a genetically determined, photoperiodically induced diapause at the end of the last larval instar (Barnes 1991). Diapausing larvae overwinter in cocoons in protected sites under bark or in debris, but a good number will remain in harvested nuts (Vail et al. 1993). The codling moth has a cosmopolitan distribution at latitudes above 25° in the northern and southern hemispheres (Barnes 1991). In California the generation time (egg to egg) averages 620 degree days (DD)°C, which results in 3 to 4 flights a year. Adults emerg-

ing in spring from overwintered larvae give rise to a first flight in spring, and their progeny emerge in two subsequent generations, in June and August, respectively. Feeding from the progeny of the first flight can cause nuts to be aborted, whereas progeny of later flights are more likely to cause internal damage to harvested nuts (Barnes 1991). Codling moth larvae are often not present in walnuts damaged by their feeding. But, in addition to direct damage, they can also provide an entry for navel orangeworm, and have been a cause for phytosanitary fumigation treatments of walnuts (Mitcham et al. 2004).

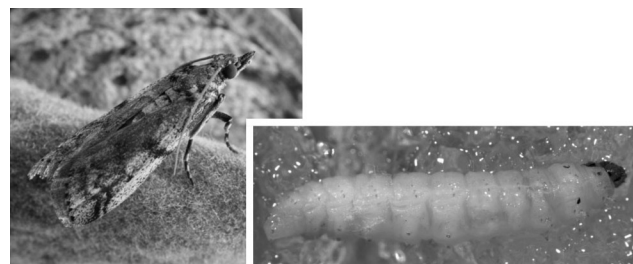


Figure 2. Navel orangeworm adult (Peggy Greb, USDA-ARS) and larva (Charles Burks, USDA-ARS).

Navel orangeworm *Amyelois transitella* (Walker)

Navel orangeworm adults have gray-brown wings with black transverse markings. Slightly over 0.5 inch long, they are superficially similar to Mediterranean flour moth (Chapter 4). Adults do not feed. Essentially a scavenger, the navel orangeworm has a wider and more taxonomically diverse host range than the codling moth, and typically feeds on fruit, nuts, and legume pods, generally in later stages of maturity or decay (Curtis and Barnes 1977). Flat, oval eggs are laid individually or in clumps on fruit or leaves near fruit, where they are glued securely. Eggs are initially cream-colored, and then turn reddish-orange before larval emergence.

Navel orangeworm larvae are poor penetrators, and typically depend on naturally occurring fissures or entry holes from other insects for access to larval hosts (Curtis and Barnes 1977). They range in color from white to orange. The sickle-shaped prothoracic spiracles distinguish navel orangeworm larvae from codling moth, but navel orangeworm and carob moth larvae share this characteristic and are difficult to distinguish (Solis 2011). Unlike codling moth, navel orangeworm larvae pupate inside host fruit or nuts rather than exiting to pupate elsewhere (Kuenen and Siegel 2010). Evidence for diapause in the last larval instar exists (Gal 1978, Legner 1983), as in other Phycitinae (Cox 1979, Bell 1994), but all larval stages are observed in overwintering populations.

Discrete flights have been described for the navel orangeworm, comprising adults emerging from overwintering larvae followed by two or more successive generations (Sanderson et al. 1989). Larval development time varies greatly for this species (Kuenen and 2010, Siegel et al. 2010). In areas of higher abundance there is overlap of flights, particularly later in the season. In addition to direct damage to products, the navel orangeworm is a target of some phytosanitary restrictions (Plant Health Australia 2009).

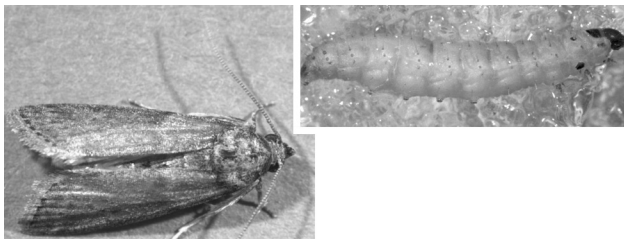


Figure 3. Carob moth adult (Joel Siegel, USDA-ARS) and larva (Charles Burks, USDA-ARS).

Carob moth *Ectomyelois ceratoniae* (Zeller)

The carob moth adult is a gray moth with a light-brown banded pattern. The adult does not feed. It is similar in size to the navel orangeworm, and larger than the Indianmeal moth, raisin moth, almond moth, and tobacco moth. The range and nature of hosts is similar to that described previously for the navel orangeworm (Cox 1979, Gothilf 1984). In particular, it is a worldwide pest of dates (Blumberg 2008) and can become a serious storage pest in almonds (Calderon et al. 1969). Like the navel orangeworm, carob moth eggs are glued directly to the host and are initially white; older eggs turn pink before hatching. Carob moth larvae, like those of the navel orangeworm, are poor penetrators and depend on openings occurring naturally or created by other pests (Gothilf 1984). They usually pupate in the fruit in which they developed, although some individuals pupate under tree bark or ground litter (Botha and Hardy 2004). In Australia this species generally overwinters in diapause (Botha and Hardy 2004), which occurs after the last larval instar (Cox 1979).

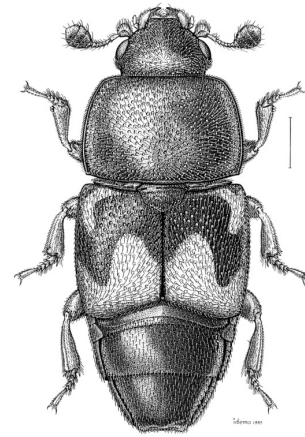


Figure 4. Driedfruit beetle adult (from Bousquet 1990).

Driedfruit beetle *Carpophilus hemipterus* (L.)

The driedfruit beetle adult is small (0.1 to 0.2 inch) and black with yellow markings on the elytra (forewings). The elytra do not completely cover the abdomen. Adults feed, and live long relative to larval development time. Rotting, fermenting, or overripe fruit are the preferred oviposition site. The driedfruit beetle is an important field pest of dried figs and dates and can infest raisins during the drying process (Simmons and Nelson 1975, Carpenter and Elmer 1978). It also feeds on a variety of other rotting fruits

(e.g., peaches and grapes), where it is usually considered of minor importance since sound fruit is not attacked.

Eggs are white, cylindrical, and 2 to 3 mm long. Larvae develop in the host, and are up to 0.25 inch, white to yellow, with two spine-like projections at the tail end. Larvae leave the host to pupate, typically in surrounding soil (Simmons and Nelson, 1975), and emerge as adults. The larval developmental period is potentially as short as 12 days. Adults live for more than 100 days at 25°C, and up to 60 days at 35°C (El-Kady et al., 1962). Unlike the previous moth species, the driedfruit beetle flies during the day and only when the temperature is above 18°C (Simmons and Nelson 1975).



Figure 5. Vinegar fly adult (Jack Kelley Clark, courtesy University of California Statewide IPM Program).

Vinegar flies *Drosophila* species

Vinegar flies (*Drosophila*) adults are small flies (0.1 inch) distinguished by bright red eyes. The species *Drosophila melangoster*, *D. simulans*, and *D. pseudoobscura* have long been associated with dried fruit production around the world (Simmons and Nelson, 1975). Adults feed, and live long relative to larvae. Vinegar flies are occasional pests of dried figs (Burks and Brandl, 2005) and raisins (Buchanan et al. 1984), but they do not infest as often as the dried-fruit beetle or navel orangeworm.

Vinegar flies often are associated with fungus or bacterial infection of figs (Simmons and Nelson 1975). Microscopic eggs are inserted into these hosts. Larvae are white to tan. Unlike the driedfruit beetle, there is no head capsule, but there are paired mouth hooks. Larvae grow up to 0.25 inch long, then pupate in drier parts of the larval host. The pupa has a yellow-brown case. Development from egg to adult can occur in as little as 7 days. Adults live 40 or more days at 20 to 25°C, with an average production of 1,000 eggs per female (Simmons and Nelson 1975). Vinegar flies are strong daytime fliers and can move

over 8 km in a day. They are less likely to fly under very strong light or with even light wind (Simmons and Nelson 1975). In California's San Joaquin Valley, abundance of these species is suppressed during the hotter part of summer, and then increases with cooling temperatures at the end of summer (Simmons and Nelson 1975).



Figure 6. Indianmeal moth adult (from Linsley and Michelbacher 1943).

Indianmeal moth *Plodia interpunctella* (Hübner)

Indianmeal moth adults are slightly under 0.5 inch; smaller than navel orangeworm and carob moth, and similar in size to almond moth, tobacco moth, and raisin moth. The Indianmeal moth is the most common and widely distributed of stored product Phycitinae, and probably causes harm in the widest variety of commodities (Simmons and Nelson 1975). It attacks a wide range of stored grains and pulses, dried fruits and nuts, dried vegetables, and processed foods (Perez-Mendoza and Aguilera-Peña 2004).

The Indianmeal moth adult is distinguished from adults of these other species by a distinct two-tone pattern of the wings (Figure 6), with the upper (proximal) part of the wings tan and the lower (distal) part copper (this pattern may be less evident in older specimens or those from a very dusty environment). Adults do not feed. Both mating and oviposition are less strictly controlled by day-night cycles compared to other stored product moths (Mohandass et al. 2007).

Eggs are white, round to ellipsoid, and more than 0.5 mm in diameter. Eggs are slightly sticky and are preferentially laid on or between host products, but frequently fall between host material rather than adhering to it (Sambaraju and Phillips 2008). When

direct access to host material is lacking, oviposition can take place nearby, and newly hatched larvae can find food up to 38 cm away (Mohandass et al. 2007). Larvae do not penetrate unbroken packaging well, but efficiently locate small openings in packing to infest packages (Mohandass et al. 2007). Mature larvae are up to 0.5 inch long with a white integument. They are distinguished from navel orangeworm and carob moth by a more pale integument, and from almond moth, tobacco moth, and raisin moth by a lack of dark sclerotized spots (pinacula) on the abdomen (Solis 2011). Larvae typically leave host material seeking enclosed sites with contact on all sides to form a cocoon and pupate. Adults emerge most frequently during the latter half of the day.

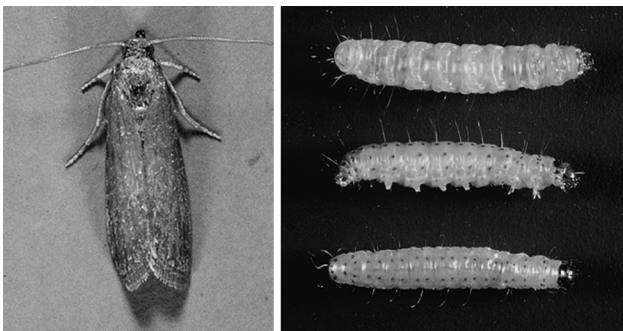


Figure 7. Almond moth adult and larvae (USDA-ARS).

Almond moth *Cadra cautella* (Walker)

Almond moth adults have light gray wings with straight dark lines, most notably near the distal edge of the forewing. The life history of the almond moth (Burgess and Haskins 1965) is similar to the Indianmeal moth, but is favored by warmer and more humid climates. In the United States, the almond moth is less abundant in California's warm, dry climate and more abundant in the warm, humid climate of the southeastern states (Soderstrom et al. 1987).

In northern Europe this species is associated with food ingredients imported from warmer climates, such as carobs, dates, and cocoa (Cox 1975b). Adults oviposit directly in the infested commodity. Eggs are similar in shape, size, and nature to the Indianmeal moth, but slightly gray instead of white. Almond moth larvae can be distinguished from those of Indianmeal moth and raisin moth by the presence of round, black pinacula (Figure 7) (Solis 2011).

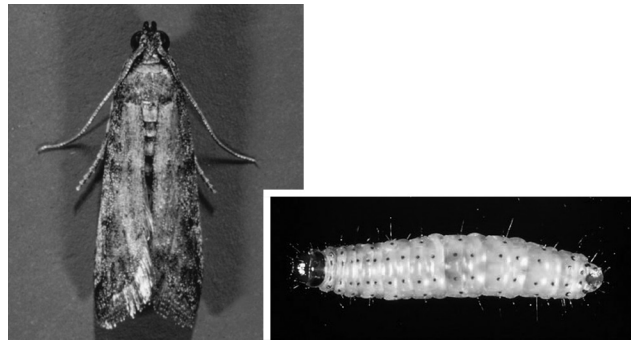


Figure 8. Tobacco moth (USDA-ARS).

Tobacco moth *Ephestia eulutella* (Hübner)

The adult tobacco moth has gray wings with more distinct black markings than the Indianmeal moth, almond moth, or raisin moth (Figure 8). The life history is generally similar to the Indianmeal moth and almond moth, but it is a more temperate species that does not develop as quickly as the Indianmeal moth or almond moth under warmer conditions, and it is rarely found in the tropics (Ashworth 1993). In particular, tobacco moth populations increase at 15°C, while those of Indianmeal moth and almond moth do not (Bell 1975).

Eggs are spherical, slightly sticky, and deposited in or near host material, as with the other moths in this group. Eggs are white initially and darken before larvae emerge. Tobacco moth larvae can be distinguished from those of Indian meal moth and raisin moth by the color and form of pinacula and surrounding cuticle, but to definitively distinguish this larva from that of the almond moth requires setal examination (Solis 2011).

While all of the species in this group (i.e., Indianmeal moth, almond moth, tobacco moth, and raisin moth) can exhibit diapause the end of the last larval instar, diapause is more intense in the tobacco moth than the Indianmeal moth or the raisin moth. Adults oviposit on cocoa in preference to grain (Ashworth 1993).

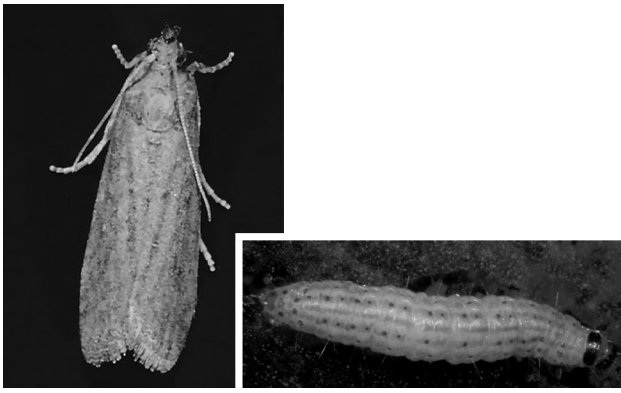


Figure 9. Raisin moth adult (USDA-ARS) and larva (Joel Siegel, USDA-ARS).

Raisin moth *Cadra figulilella* (Gregson)

The raisin moth adult can often be distinguished from related stored product moths by light pink scales on the forewing (Figure 9). Adults do not feed. The raisin moth is primarily a field pest that attacks mature or overripe fruit (Donohoe et al. 1949, Cox 1974). It is occasionally found in dried fruits and nuts, but there is no evidence that it is able to maintain or increase its population in storage (Cox 1974). The raisin moth is found primarily in the Mediterranean and similar climates in the Americas and Australia. In the United States, it is endemic in California but associated with commerce elsewhere (Donohoe et al. 1949, Cox 1975b).

Eggs are small, round, and slightly yellow-orange. Like the previous three species, eggs are sticky but generally not glued to host material. In central California, raisin moth larvae are found in a wide variety of fallen fruit (Donohoe et al. 1949). More recently they have also been found in mature almonds, but usually are not of concern because they feed on the hull rather than the nut. Raisin moth larvae can be distinguished from those of related species by the tan lines running horizontally along the back (Figure 9). Larvae leave the host before pupation and seek a suitable harborage in which to cocoon and pupate. In the orchard this is typically under the bark near the base of a tree or vine, or in adjacent soil near the surface (Donohoe et al. 1949).

This species overwinters in the last larval instar (Donohoe et al. 1949), presumably in diapause (Cox 1975a). Younger larvae usually do not successfully overwinter (Donohoe et al. 1949). Adults do not fly at less than 13°C and have limited flight at 13°C to 15°C. Field studies in central California in the 1930s found adult activity from April to November, with peak abundance in September and October. There was evidence of three flights and a partial fourth but, because host material was varied and plentiful, the species was abundant throughout the period of adult activity (Donohoe et al. 1949).

Behavior

Insect infestation of dried fruit and nuts, and detection of this infestation, is determined in part by adult behavior, including mating and aggregation, dispersal, and ovipositional preferences. In moths the female releases sex pheromone, and males find females using this scent trail. The codling moth, navel orangeworm, and carob moth each have distinct pheromone blends, whereas the remaining moths are attracted by the same principle component (El-Sayed 2011).

Each of these moth species has a relatively short adult life (Table 2) and feed only as larvae. In the codling moth, most individuals disperse short distances, but a few may travel further than 5 km (Schumacher et al. 1997). On average, mated females fly farthest 2 days after adult emergence but four-day-old unmated females fly farther, suggesting that inability to find a mate is one factor that causes long-distance dispersal in this species (Schumacher et al., 1997). In addition to pheromones for locating mates over large distances, the Indianmeal moth and almond moth use ultrasound in courtship at closer range (Trematerra and Paven 1995, Nakano 2009).

Food volatiles often play a role in the attraction of pests to a product. Mated Indianmeal moth and almond moth females are more responsive to chocolate odors in a wind tunnel compared to unmated females of these species (Olsson et al. 2005) and in the field, the vast majority of navel orangeworm females captured in traps baited with almond meal are mated (Burks et al. 2009). These observations suggest that females of the phycitid moths discussed

in this chapter generally mate first, and then disperse for oviposition.

In the oligophagous codling moth, eight volatiles have been identified as host cues, and there seems to be some plasticity in female response to these volatiles in the field (Witzgall et al. 2005). One of these compounds, pear ester, captures both male and female codling moths in the field, and the proportion of sexes captured varies with factors such as cultivated variety and trap type (Knight et al. 2011).

The other moth pests discussed in this chapter generally have a wider host range. Carob moth females are attracted by a compound associated with fungal infection of dates (Cossé et al. 1994), and phenyl propionate, a compound sometimes associated with plant breakdown products, is attractive to the navel orangeworm (Burks et al. 2009). The navel orangeworm is also attracted by host-associated oils (Phelan et al. 1991), as is the Indianmeal moth (Sambaraju and Phillips 2008). In the Indianmeal moth, tactile cues are also important in stimulating oviposition (Sambaraju and Phillips 2008).

In the driedfruit beetle and vinegar flies, males and females locate each other and food resources via a synergistic attraction to food odors and aggregation pheromones produced by males. In the driedfruit beetle the aggregation pheromone is a blend of 13- to 15-carbon molecules, released by males and attractive to both males and females (Bartelt et al., 1992). Similar pheromones are produced by the related and often coexisting species, *Carpophilus freemani* and *C. mutilatis* (Bartelt et al. 1995). These aggregation pheromones have little effect by themselves, but the pheromone in combination with volatile alcohols, esters, and acids produced by food sources the pheromone is far more attractive than either by itself (Dowd and Bartelt 1991, Blumberg et al. 1993).

Vinegar flies also use a combination of host volatiles and aggregation pheromone. Long-range host-associated cues are primarily acetic acid and similar compounds associated with vinegar (Becher et al. 2010). At closer range mating and oviposition in *Drosophila* is influenced by aggregation pheromone and other pheromones associate with the cuticle. Generally these are produced by males, but in some cases passed to females during mating (Wertheim et al. 2002, Dahanukar and Ray 2011).

Ecology

The number and abundance of species associated with dried fruits and nuts is determined principally by abiotic and host-associated factors and control measures, in part because there is usually a very low tolerance for insects associated with these high-value food items. Factors such as host nutrition and condition, processing methods, field and storage temperatures, day-length, and other storage organisms influence the development and survival of pest populations, and their economic impact.

Host suitability and moisture requirements

Various factors determine whether an insect pest can establish or increase population in postharvest conditions. Nutritional requirements are an obvious factor. Survival and development time can also be affected profoundly by the state or maturity of the host, and by the type of host, as demonstrated in studies of the Indianmeal moth (Johnson et al. 1995), the carob moth (Nay and Perring 2008), and the navel orangeworm (Siegel et al. 2010). Moisture requirements are another important variable. The almond moth has greater moisture requirements than the Indianmeal moth at similar temperatures (Burgess and Haskins, 1965, Arbogast 2007a), and also benefits more from access to water as adults (Hagstrum and Tomblin 1975).

Storage of large amounts of a commodity can provide a heterogeneous environment (e.g., more fines, broken product, or pockets of fungal infection) that may allow the presence of a pest that cannot develop on small samples of the same commodity under laboratory conditions. This observation has been dubbed the host paradox (Arbogast et al. 2005). Indianmeal moth, for example, does poorly in the laboratory on dried fruits such as raisins or prunes when compared to almonds, walnuts or pistachios (Johnson et al. 1995, 2002), and yet it is still of greatest concern for dried fruit processors. Another situation occurs when certain processing activities—such as partial rehydration of dried fruit during packing—attracts oviposition by field pests such as the driedfruit beetle or raisin moth, resulting in returns of shipments for these pests even though they normally cannot maintain a population on these commodities at that point in the marketing chain.

Table 2. Life history characteristics of selected insect pests of dried fruits and nuts species.

	Lower and Upper Develop- mental Limits (°C)	Developmental Time (Egg to Adult, Days)	Lifetime Fecundity (Eggs/Female)	Adult Longevity (Days)	References
Codling moth <i>Cydia pomonella</i>	18 to 34	38 at 26°C	160	10	(14; 18)
Navel orangeworm <i>Amyelois transitella</i>	13 to 34	32 at 26°C	200	11	(6; 12; 15)
Carob moth <i>Ectomyelois ceratoniae</i>	13 to 38	32 at 25°C	200	7	(7; 13)
Driedfruit beetle <i>Carpophilus hemipterus</i>	20 to 42	12 at 35°C	>1,000	103	(9; 16)
Vinegar fly <i>Drosophila</i> spp.	9 to 30	7 at 26°C	750	25	(16)
Indianmeal moth <i>Plodia interpunctella</i>	>15 to >30	26 at 30°C	200-365	11	(1; 8; 10; 11)
Almond moth <i>Cadra cautella</i>	>15 to >30	28 at 30°C	400-500	10	(2; 3)
Tobacco moth <i>Ephestia elutella</i>	<15 to <30	33 at 30°C	≈200	12	(2; 19)
Raisin moth <i>Cadra figulilella</i>	15 to 36	43 at 28°C	351	16	(4; 5; 17)

References cited: 1) Arbogast 2007b. 2) Bell 1975. 3) Burges and Haskins 1965. 4) Cox 1974. 5) Donohoe et al. 1949. 6) Engle and Barnes 1983. 7) Gothilf 1969. 8) Huang and Subramanyam 2003. 9) James and Vogle 2000. 10) Johnson et al. 1995. 11) Johnson et al. 1992. 12) Kellen and Hoffmann 1983. 13) Nay and Perring 2008. 14) Pitcairn et al. 1992. 15) Seaman and Barnes 1984. 16) Simmons and Nelson 1975. 17) Subramanyam and Hagstrum 1993. 18) Vickers 1997. 19) Waloff et al. 1948.

Temperature and diapause

The effect of temperature on development has been examined using various approaches. For field pests, degree-day models tend to be used. These models assume daily fluctuation in temperature. The upper and lower developmental threshold determined in these model are ultimately parameters in a model that are of interest primarily for their ability to predict development at intermediate temperatures.

Another approach that has been used in stored product pests is to determine empirically the ability of populations to grow at various constant temperatures of interest. This latter approach implies that populations of interest experience something close to constant temperature, an assumption that is more likely to be met in stored products than in field situations. As a result, a model for the population development for the almond moth includes an implied developmental threshold of 12°C, although empirical studies find that this species does not develop from egg to adult at 15°C under favorable conditions of diet and

moisture content (Bell 1975) (Table 2). Temperature ranges for development are one reason that the almond moth is considered a predominantly tropical species (Cox 1975b), and the tobacco moth a predominantly temperate species (Ashworth 1993). The driedfruit beetle develops at higher temperatures than the other *Carpophilus* spp., *C. freemani* and *C. mutilatis* (James and Vogle 2000). This higher temperature tolerance, along with the high temperatures encountered in production of sun-dried figs, may explain why *C. freemani* and *C. mutilatis* comprise 40% of the nitidulids trapped with tri-species traps in fig orchards (C. S. Burks, unpublished data), but were rarely trapped in trapping in the substandard fig warehouse (Johnson et al. 2000).

Diapause is another factor that can influence geographical range. There is evidence that all of the moth species discussed in this chapter can be induced by environmental conditions into diapause at the end of the last larval instar (Bell 1994). Diapause is a genetically plastic characteristic; it may assist the codling moth in adapting to local host

availability (Barnes 1991), and can vary in presence, prevalence, and intensity in the Indianmeal moth (Mohandass et al. 2007). Despite genetic plasticity, diapause is a factor in limiting the range of the raisin moth (Cox 1975a and b) and the codling moth (Willett et al. 2009). Because diapausing larvae are often the stage most tolerant to disinfestation treatments, particularly fumigation (Bell and Glanville 1973, Tebbets et al. 1986), their occurrence in product may affect control efficacy.

Generations and seasonal abundance

Discrete cohorts are a logical result of a short adult life relative to larval development time, as occurs with the moth pests described in this chapter. This tendency toward a discrete cohort structure can be reduced in the presence of prolonged development on a poor host. For example, both the development time and variation in development time were greater for the Indianmeal moth on dried fruit compared to tree nuts (Johnson et al. 1995). In a substandard dried fig pool, where no attempt was made to control pest populations, the two peaks of activity occurred after diapause termination in spring and in late summer when higher-quality host material was first added with new-season dried figs (Johnson et al. 2000). In the carob moth, discrete cohorts were seen in almonds (Gothilf 1984, Botha and Hardy 2004), but less so in dates (Nay and Perring 2008), where stages and host quality was more variable.

Natural enemies

Dried fruit and nut pests have a number of parasites, predators, and pathogens that may reduce pest populations. Insecticide applications timed to conserve parasite populations and release of *Trichogramma* egg parasites are important parts of integrated pest management for field pests such as codling moth and navel orangeworm (Strand 2003). Research into use of these organisms in the storage environment focuses on the use of microbial pesticides or inundative release of parasites (Brower et al. 1995), generally targeting postharvest pyralids. The most commonly studied parasites are *Habrobracon hebetor* (Say), *Venturia canescens* (Gravenhorst), and *Trichogramma pretiosum* Riley (Brower et al. 1988, 1990, Press et al. 1982). Predatory bugs such as *Xylocoris flavipes* (Reuter) are also common (Bower 1990).

Because of the low tolerance for live insects in dried fruits and nuts, it is unlikely that parasite or predators would ever be sufficient to control pest populations. It was noted that naturally occurring *H. hebetor* populations were capable of dramatically reducing Indianmeal moth populations in stored raisins (Johnson et al. 2002). Johnson et al (2000) demonstrated that *H. hebetor* was active throughout the winter in a substandard fig warehouse in central California, and suggested that winter parasite releases could reduce spring emergence of Indianmeal moth adults.

Within the United States, actual release of natural enemies into bulk stored dried fruits and nuts is considered food adulteration and not allowed, although exemptions for bulk stored grain and packaged products have been obtained (Anonymous 1992). Commercially available microbial insecticides containing *Bacillus thuringiensis* Berliner were used for control of moth species both in storage and in the orchard, but resistance to the bacterium has developed in Indianmeal moth populations, decreasing its effectiveness for this pest (McGaughey 1985, Brower et al. 1990). A microbial insecticide containing the Indianmeal moth granulosis virus was shown to be effective in protecting walnuts (Johnson et al. 1998), almonds, and raisins (Johnson et al. 2002) against damage, even under heavy population pressure.

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