Mini Risk Assessment
Chestnut weevil, *Curculio elephas* (Gyllenhal)
[Coleoptera: Curculionidae]

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September 19, 2003

Introduction

Curculio elephas is an oligophagous pest, attacking several species of chestnut (*Castanea* spp.) and oak (*Quercus* spp.). This weevil is generally distributed in Europe and portions of North Africa and the Middle East (USDA 1983). The insect is considered a somewhat specialized, but still economically significant, pest. To our knowledge the risks posed by this pest for US agriculture and native ecosystems have not been evaluated previously in a formal pest risk assessment.

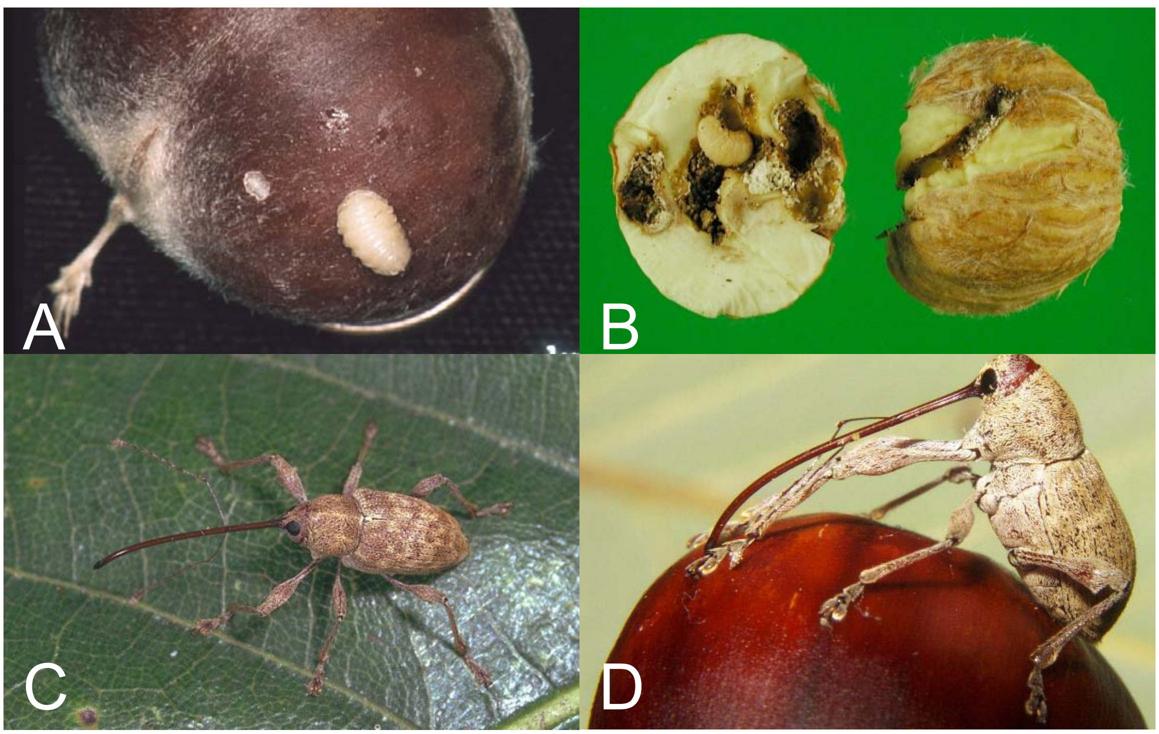


Figure 1. Life stages of *Curculio elephas*: A) Larva on surface of chestnut (image from: Jerry A. Payne, USDA ARS, www.invasive.org); B) Larva and associated damage inside chestnut (image from: http://www.pierroton.inra.fr/IEFC/bdd/patho/patho_affiche.php?langue=en&id_fiche=6); C) Adult on surface of chestnut leaf (image from: http://www.inra.fr/Internet/Produits/HYPPZ/IMAGES/7031480.jpg); D) Adult on surface of chestnut (image from: F. Köhler, http://www.koleopterologie.de/gallery/fhl11/curculio-elephas-foto-koehler.html).

1. **Ecological Suitability. Rating: High.** *Curculio elephas* is currently found in the eastern Palearctic (USDA 1983). This region is generally characterized by a temperate climate (CAB 2000). The currently reported global distribution of

C. elephas suggests that the pest may be most closely associated with temperate broadleaf and mixed forests and temperate coniferous forests. Based on the distribution of climate zones in the US, we estimate that approximately 47% of the continental US would be suitable for *C. elephas* (Fig. 2). See Appendix A for a more complete description of this analysis.

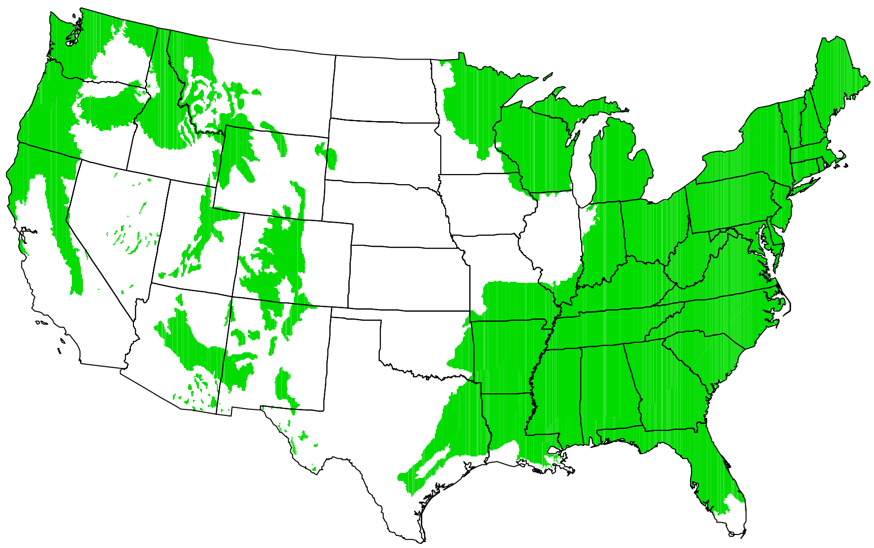


Figure 2. Predicted distribution of *Curculio elephas* in the continental US.

2. **Host Specificity/Availability. Rating: Medium/Medium.** Larvae of *Curculio elephas* feed and develop within chestnuts (*Castanea* spp.) and acorns (*Quercus* spp.) (Debouzie et al. 1996, Ploye and Menu 2000, INRA 2003a). Many plant species within these genera are commonly grown and/or occupy forests in much of the US (USDA 2001). Reported host plants include: European chestnut (*Castanea sativa*), sweet chestnut (*C. vesca*), cork oak (*Quercus suber*), and pudunculate oak (*Q. robur*) (Canakcioglu 1969, CAB 2000, Branco et al. 2001, Debouzie et al. 2002).

   See Appendix B for maps describing where various hosts are grown commercially in the US.

3. **Survey Methodology. Rating: Low**. Surveys for *C. elephas* must typically depend on emergence traps or visual inspection of potentially infested chestnuts or acorns. During visual inspections, nuts must be opened to reliably detect larvae (USDA 1983). Because of difficulties in reliably identifying immature stages of the insect, any curculionid identified during a survey of chestnuts or acorns should be reared to an adult (USDA 1983).

   Emergence traps may also be used to collect newly emerged adults (Hrašovec 1993). In one case, the emergence trap was an inverted 1m^2 wooden box; holes in

the side of each box provided light to which the insects were attracted (Menu and Debouzie 1993). Adults were captured in small cages attached to the box by a plastic tube.
Near Lyon, France, emergence occurs between late August and October (Ploye and Menu 2000). However, the timing of adult emergence is very location specific, and adults may emerge from June through September (USDA 1983). Approximately one week following emergence, eggs are oviposited only inside acorns or chestnuts, where larvae feed and develop, then exit to overwinter underground in soil (Menu 1993a, Menu and Debouzie 1995, Desouhant et al. 1998).

No sex nor aggregation pheromone has yet been identified for *Curculio elephas*. However, "male-specific compounds" that attract females and some males have been identified for the pecan weevil, *Curculio caryae* (Bartlelt 1999). The aggregation pheromone of *C. caryae* is a five component blend of grandisol and isomers of ochtodenol (Hedin et al. 1997). Four of these compounds are also used by boll weevil (Bartlelt 1999). No work has been conducted to develop or adapt a pheromone-baited trap for *C. elephas*.

4. **Taxonomic Recognition**. **Rating: Medium.** *C. elephas* is described as follows:
    - "Adult: "6 to 9 mm long, yellowish to greyish, covered in a thick pubescence; rostrum slender, strongly curved, and that of the female as long as the body
    - Larva: 15 mm long, apodous, thick, curved, creamy white; head brown" (INRA 2003a).

    In the US, larvae and adults of *C. elephas* are most likely to be confused with other *Curculio* spp. that also feed on chestnuts. Two native or naturalized *Curculio* spp., *C. caryatrypes* and *C. sayi*, may also affect chestnuts, but adults of these taxa are easily distinguished from *C. elephas*. In addition, other weevils of the genus *Conotrachelus* (*C. carnifer* and *C. posticatus*) may develop in chestnut and complicate surveys for *C. elephas*. From Europe, taxa that might be confused with *C. elephas* include *C. nucum* and *C. glandium*, though the latter species is more commonly associated with acorns (USDA 1983). No taxonomic keys are available to identify Curculionidae pupae to genus or species, and distinguishing features of many immature *Curculio* spp. have not been described (USDA 1983). For detailed descriptions and distinguishing characteristics of adult *Curculio* spp., see USDA (1983).

5. **Entry Potential. Rating: High.** Interceptions of *C. elephas* or "*Curculio* sp." have been reported 11,767 times since 1985, primarily on acorns and chestnuts (USDA 2003). Annually, about 622 (±61 standard error of the mean) interceptions of *C. elephas* or "*Curculio* sp." are reported (USDA 2003). Historically, interceptions have been associated predominately with international airline passengers (97%). Although the pest has been intercepted at 55 ports of entry in the United States, the majority of interceptions have been reported from Los Angeles (25%), Honolulu (25%), JFK International Airport (13%), Chicago

(6%), and San Francisco (5%). These ports are the first points of entry for cargo or airline passengers coming into the US and do not necessarily represent the intended final destination of infested material. Movement of potentially infested material is characterized more fully later in this document.

Curculio elephas or *Curculio* sp. has been listed with 57 plant taxa (USDA 2003). However, 95% of all interceptions listed some species of chestnut (*Castanea* spp.) as the host, 4% listed acorns from some species of oak (*Quercus* spp.).

6. **Destination of Infested Material. Rating: High.** When an actionable pest is intercepted, officers ask for the intended final destination of the conveyance. Cargo or passengers with materials infested with *C. elephas* or "*Curculio* sp." were destined for 48 states (including the District of Columbia) (USDA 2003). The most commonly reported destinations were California (33%), Hawaii (24%), New York (11%), Illinois (11%), and Texas (4%). We note that some portion of each of the four states in the continental US has climate and hosts that would be suitable for establishment by *C. elephas*.

7. **Potential Economic Impact. Rating: Medium.** *Curculio elephas* is an economically important pest causing damage to fruits of chestnut and oak (Bürgés and Gál 1981, Debouzie et al. 1996, Branco et al. 2001). This weevil is one of the most serious pests of European chestnut (*Castanea sativa*) in Europe; damage is caused by adults feeding on the base of young nuts and larvae feeding on mature nuts (USDA 1983). Damage can be variable depending on the chestnut variety (INRA 2003a). Adult feeding can cause up to 20% premature nut drop while combined larval and adult feeding can cause up to 90% crop loss (USDA 1983, Paparatti and Speranza 1999, INRA 2003a, b). Larval feeding damage on acorns can have a negative effect on seedling vigour (Branco et al. 2001). The percentage of attacked acorns in Portugal is estimated between 50 – 63%, of which 89 – 95% of the damage causing pest population is *C. elephas* (Branco et al. 2002). Although infested acorns are still able to germinate and survive, there are little reserves left for seedling growth (Branco et al. 2002). Thus, the pest may impede regeneration of oak and chestnut stands.

   We also speculate that *C. elephas* may adversely the health of chestnut by interacting with *Endothia parasitica*, the causal agent of chestnut blight. Although there are no reports of *C. elephas* vectoring the pathogen or predisposing trees to infection, Russin et al. (1984) noted that ~42% of native curculionids (i.e., *Acoptus suturalis* and *Rhyncolus brunneus*) carried the pathogenic fungus. Pakaluk and Anagnostakis (1997) conjecture that *A. suturalis* may vector the pathogen.

   Damage to chestnut and acorn is widespread throughout Europe with reports of significant damage from Algeria (Chakali et al. 2002), Italy (Paparatti and Speranza 1999), Poland (Pomorski and Tarnawski 1980), Portugal (Menu and

Debouzie 1993, Branco et al. 2001), Spain, and Turkey (Yaman et al. 1999) (Canakcioglu 1969)

8. **Establishment Potential. Rating: Medium.** Despite the large number of *C. elephas* that are introduced into the US each year, no occurrences of the pest have been reported in the wild. The most difficult challenge for an invading population of *C. elephas* would be locating a suitable host. Although populations of oak and chestnut can be dense in some areas, adult *C. elephas* are generally considered poor dispersers. Thus, newly arrived individuals (most likely as larvae in infected nuts) must leave the nut, pupate in the soil (occasionally, but rarely, in the nut), emerge and locate a host. Unless a host is in the vicinity of the introduction site, the likelihood of locating a suitable host seems limited.

   See Appendix C for a more complete description of the biology of *C. elephas*.

References:

Bartlelt, R. J. 1999. Weevils, pp. 91-112. *In* J. Hardie and A. K. Minks [eds.], Pheromones of non-lepidopteran insects associated with agricultural plants. CABI Publishing, New York. PDF

Branco, M., C. Branco, H. Merouani, and M. Almeida. 2001. Germination success, survival and seedling vigour of *Quercus suber* acorns in relation to insect damage. Forest Ecology and Management 166: 159-164. PDF

Branco, M., C. Branco, H. Merouani, and M. Almeida. 2002. Effect of insect predation on the quality and storage conditions of acorns in cork oak (*Quercus suber* L.). Integrated Protection in Oak Forests 25: 163-167. PDF

Bürgés, V., and T. Gál. 1981. As to the spreading and manner of life of *Cucurlio elephas* Gyll. (Col., Curculionidae) in Hungary, Part 1: Spreading, damaging, swarming and sex proportions. Journal of Applied Entomology/Zeitschrift für Angewandte Entomologie 91: 375-382. PDF

CAB. 2000. Crop protection compendium:global module. Commonwealth Agricultural Bureau International, Wallingford, UK.

Canakcioglu, H. 1969. Insect damage on cones and seeds of forest trees in Turkey. Istanbul Universitesi Orman Fakultesi Dergisi 19A: 83-90.

Chakali, G., A. Attal-Bedreddine, and H. Ouzani. 2002. Insect pests of the oaks *Quercus suber* and *Q. ilex* in Algeria. Integrated Protection in Oak Forests 25: 93-100. PDF

Debouzie, D., and C. Pallen. 1987. Spatial distribution of chestnut weevil *Balaninus* (=*Curculio*) *elephas* populations. International Symposium on Insect-Plant Relationships: 77-83. PDF

Debouzie, D., A. Heizmann, E. Desouhant, and F. Menu. 1996. Interference at several temporal and spatial scales between two chestnut insects. Oecologia 108: 151-158. PDF

Debouzie, D., E. Desouhant, F. Oberli, and F. Menu. 2002. Resource limitation in natural populations of phytophagous insects. A long-term study case with the chestnut weevil. Acta Oecologica 23: 31-39. PDF

Desouhant, E. 1996. Oviposition in the chestnut weevil, *Cucurlio elephas* Gyll. (Coleoptera: Curculionidae). Annales de la Societe Entomologique de France 32: 445-450. PDF

Desouhant, E. 1998. Selection of fruits for oviposition by the chestnut weevil, *Cucurlio elephas*. Entomologia Experimentalis et Applicata 86: 71-78. PDF

Desouhant, E., D. Debouzie, and F. Menu. 1998. Oviposition pattern of phytophagous insects: on the importance of host population heterogeneity. Oecologia 114: 382-388. PDF

Hedin, P. A., D. A. Dollar, J. K. Collins, J. G. DuBois, P. G. Mulder, G. H. Hedger, M. W. Smith, and R. D. Eikenbary. 1997. Identification of male pecan weevil pheromone. Journal of Chemical Ecology 23: 965-977.

Hrašovec, B. 1993. Biology of the insects of the genus *Balaninus* Germ., an acorn pest of the pedunculate oak (*Quercus robur* L.). Glasnik za sumske pokuse 29: 1-38. PDF

INRA. 2003a. *Curculio elephas* (Gyllenhal) Chestnut weevil. Institut National de la Recherche Agronomique / HYPPZ on line. www.inra.fr/Internet/Produits/HYPPZ/RAVAGEUR/6curele.htm.

INRA. 2003b. Chestnut *Castanea sativa* Miller (Fagaceae). Institut National de la Recherche Agronomique / HYPPZ on line. www.inra.fr/Internet/Produits/HYPPZ/CULTURES/6c---042.htm.

Manel, S., and D. Debouzie. 1995. Prediction of egg and larval development times in the field under variable temperatures. Acta Oecologica 16: 205-218. PDF

Manel, S., and D. Debouzie. 1997. Modeling insect development time of two or more larval stages in the field under variable temperatures. Environmental Entomology 26: 163-169. PDF

Menu, F. 1993a. Diapause development in the chestnut weevil *Cucurlio elephas*. Entomologia Experimentalis et Applicata 69: 91-96.

Menu, F. 1993b. Strategies of emergence in the chestnut weevil *Cucurlio elephas* (Coleoptera: Curculionidae). Oecologia 96: 383-390. PDF

Menu, F., and D. Debouzie. 1993. Coin-flipping plasticity and prolonged diapause in insects: example of the chestnut weevil *Cucurlio elephas* (Coleoptera: Curculionidae). Oecologia 93: 367-373. PDF

Menu, F., and D. Debouzie. 1995. Larval development variation and adult emergence in the chestnut weevil *Cucurlio elephas* Gyllenhall (Col., Curculionidae). Journal of Applied Entomology/Zeitschrift für Angewandte Entomologie 119: 279-284. PDF

Menu, F., J.-P. Roebuck, and M. Viala 2000. Bet-hedging diapause strategies in stochastic environments. The American Naturalist 155: 724-734. PDF

Olson, D. M., E. Dinerstein, E. D. Wikramanayake, N. D. Burgess, G. V. N. Powell, E. C. Underwood, J. A. D'Amico, I. Itoua, H. E. Strand, J. C. Morrison, C. J. Loucks, T. F. Allnutt, T. H. Ricketts, Y. Kura, J. F. Lamoreux, W. W. Wettengel, P. Hedao, and K. R. Kassem. 2001. Terrestrial ecoregions of the world: a new map of life on earth. BioScience 51: 933-938. PDF

Önuçar, A., and O. Ulu. 1989. Izmir ili çevresindeki kestane yetistirme alanlarinda fauna tespiti ve meyvelerde kurtlanmaya neden olan zararlilar ile savasim olanaklari üzerinde arastirmalar. [Faunistic survey studies in chestnut plantations and establishment of control measures against the infectious pest in nuts in Izmir]. Doga Bilim Dergisis 13: 637-643. PDF

Pakaluk, J., and S. L. Anagnostakis. 1997. *Acoptus suturalis* LeConte (Coleoptera: Curculionidae: Zygopinae), a potential vector of the chestnut blight fungus, *Cryphonectria parasitica* (Murrill) Barr, in the eastern United States. Proceedings of the Entomological Society of Washington 99: 583-584.

Paparatti, B., and S. Speranza. 1999. Biological control of chestnut weevil (*Cucurlio elephas* Gyll.; Coleoptera, Curculionidae) with the entomopathogen fungus *Beauveria bassiana* (Balsamo) Vuill. (Deuteromycotina, Hyphomycetes). Acta Horticulturae 494: 459-464. PDF

Ploye, H., and F. Menu. 2000. Clutch size manipulations in the chestnut weevil, *Cucurlio elephas*: fitness of oviposition strategies. Oecologia 122: 493-499. PDF

Pomorski, R. J., and C. Tarnawski. 1980. A new station of *Curculio elephas* Gyllenhal, 1836 (*Col., Curculionidae*) in Poland. Przeglad Zoologiczny 23: 213-214. PDF

Russin, J. S., L. Shain, and G. L. Nordin. 1984. Insects as carriers of virulent and cytoplasmic hypovirulent isolates of the chestnut blight fungus. Journal of Economic Entomology 77: 838-846.

Soula, B., and F. Menu. 2003. Variability in diapause duration in the chestnut weevil: mixed ESS, genetic polymorphism or bet-hedging? Oikos 100: 574-580. PDF

Speranza, S. 1999. Chestnut pests in central Italy. Acta Horticulturae 494: 417-423. PDF

USDA. 1983. Pests not known to occur in the United States or of limited distribution, No. 32: European chestnut weevil, pp. 1-10. APHIS, PPQ, Hyattsville, MD. PDF

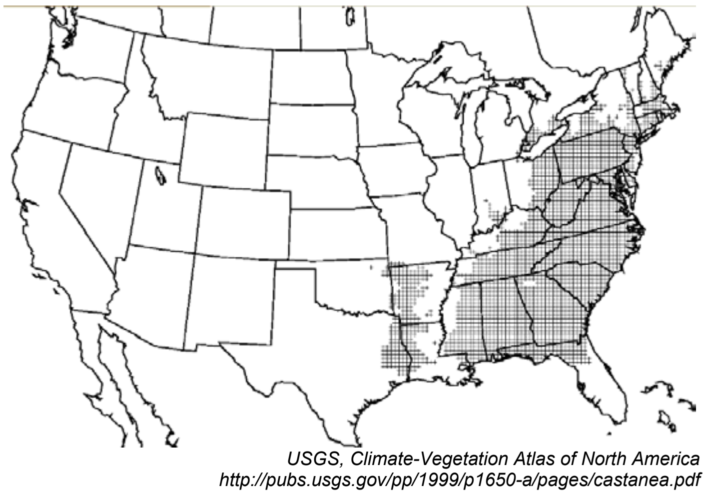
USDA. 2001. The PLANTS database, ver. 3.5. National Plant Data Center, USDA-Natural Resources Conservation Service. http://plants.usda.gov.

USDA. 2003. Port Information Network (PIN-309): quarantine status database. US Department of Agriculture, Animal and Plant Health Inspection Service, Plant Protection and Quarantine, Riverdale, MD. restricted access database.

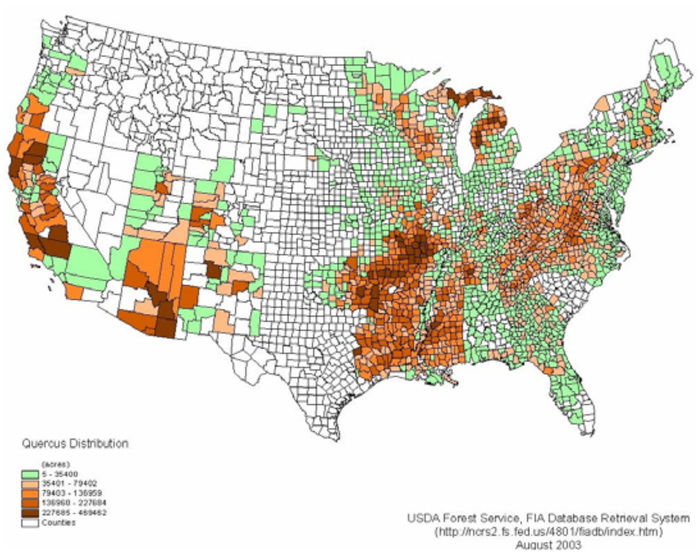
Yaman, M., Z. Demirbað, and A. O. Beldüz. 1999. Investigations on the bacterial flora as a potential biocontrol agent of chestnut weevil, *Curculio elephas* (Coleoptera: Curculionidae) in Turkey. Biologia Bratislava 54: 679-683. PDF

Appendix A. Comparison of climate zones. To determine the potential distribution of a quarantine pest in the US, we first collected information about the worldwide geographic distribution of the species (CAB 2000). We then identified which biomes (i.e., habitat types), as defined by the World Wildlife Fund (Olson et al. 2001), occurred within each country or municipality reported for the distribution of the species. Biomes were identified using a geographic information system (e.g., ArcView 3.2). An Excel spreadsheet summarizing the occurrence of biomes in each nation or municipality was prepared. The list was sorted based on the total number of biomes that occurred in each country/municipality. The list was then analyzed to determine the minimum number of biomes that could account for the reported worldwide distribution of the species. Biomes that occurred in countries/municipalities with only one biome were first selected. We then examined each country/municipality with multiple biomes to determine if at least one of its biomes had been selected. If not, an additional biome was selected that occurred in the greatest number of countries or municipalities that had not yet been accounted for. In the event of a tie, the biome that was reported more frequently from the entire species' distribution was selected. The process of selecting additional biomes continued until at least one biome was selected for each country. The set of selected biomes was compared to the occurrence of those biomes in the US.

Appendix B. Commercial production of hosts of *Curulio elephas* in the continental US..



Map 1. Chestnut (*Castanea* spp.)



Map 2. Oak (*Quercus* spp.)

Appendix C. Biology of *Curculio elephas*

Population phenology

Curculio elephas is a univoltine species that develops in chestnuts and acorns (Debouzie and Pallen 1987, Speranza 1999, Ploye and Menu 2000, INRA 2003a, Soula and Menu 2003). Adults feed on young nuts (USDA 1983). The majority of damage is attributed to larvae. This weevil has a unique life cycle (Fig. C1, Hrašovec 1993, Speranza 1999). Dispersal and overall mobility are limited, and the weevil remains in or near the fruit (i.e., nuts) of its host plant –or the host plant itself- throughout its life (Debouzie and Pallen 1987, Menu et al. 2000, Debouzie et al. 2002). Adults emerge underneath the host tree, fly to nuts, and mate; females then oviposit inside the nuts of the tree under which they emerged (Debouzie and Pallen 1987). Larvae complete development inside the nut. As late instar larvae, they emerge from the nut or wait until the nut drops to the ground, then they burrow into soil under the tree to enter diapause (USDA 1983, Debouzie and Pallen 1987). Larvae enter diapause between October and December (Speranza 1999) to survive challenging environmental conditions (Menu and Debouzie 1993). Further larval development begins in March and continues until adults emerge. Some larvae can delay development and remain in the soil for more than one year (Paparatti and Speranza 1999, Speranza 1999). See sections on life-stage specific biology (below) for additional details.

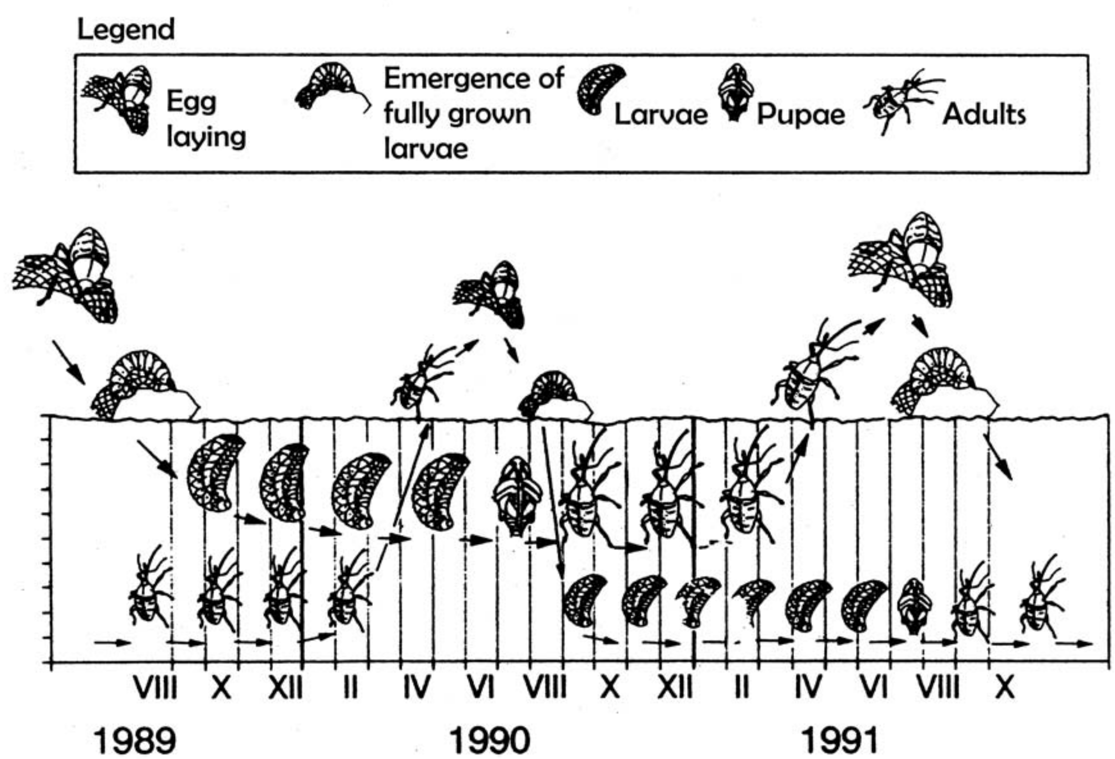


Figure C1. Population phenology of *Curculio elephas* in Croatia from 1989 to 1991. [Reproduced from Hrašovek (1993)]

Stage specific biology

Adults Adult emergence can occur between June and November, though emergence from August to September is more typical in much of Europe (USDA 1983, Menu 1993b, Menu and Debouzie 1993, Speranza 1999, Menu et al. 2000, Ploye and Menu 2000). The broad window of emergence is partially explained by the range in dates when larvae have been observed to burrow into soil --between October and November of the preceding year-- (Speranza 1999). "A newly emerged adult remains in the overwintering chamber for three to four weeks" (Paparatti and Speranza 1999).

After emergence the adult feeds for a week (INRA 2003a) by puncturing young acorns or chestnuts (USDA 1983). Mating and oviposition begin in August and continue until September (Ploye and Menu 2000, Soula and Menu 2003). Oviposition takes place on mature nuts or acorns (USDA 1983). The female is active throughout the oviposition period, which can last several weeks (USDA 1983). Females do not select nuts for oviposition based on the size of the nut, nor does the presence of other eggs or larvae of the species deter oviposition (Desouhant 1998).

In the field, adult females lived an average of 9.5 days while in protected laboratory conditions female lifespan increased to 21 to 28 days (Desouhant 1996, Debouzie et al. 2002).

Eggs Eggs are most often laid singly within holes in the chestnut, not on the leaves or branches of the tree (USDA 1983, Ploye and Menu 2000, Soula and Menu 2003). Females puncture the nut with their rostrum and deposit eggs into the hole (Speranza 1999). Multiple eggs may be inserted into a single nut. A third of the time, females oviposit in previously bored holes, thus saving energy and time (Desouhant 1996). Each females can lay 20-50 eggs, with an average of 43 eggs (USDA 1983, Ploye and Menu 2000, INRA 2003a). Females can lay an average of 1.9 eggs each day for the first 10 days after emergence (Ploye and Menu 2000).

Larvae There are four instars (Ploye and Menu 2000). Typically, one or two larvae will be located in each nut, although as many as 19 larvae have come from a single nut (USDA 1983, Paparatti and Speranza 1999, Ploye and Menu 2000, Debouzie et al. 2002). Larval development is completed inside the fruit (selected by the female) (Menu et al. 2000, Ploye and Menu 2000, Soula and Menu 2003). In time, the infested nut or the mature larva itself will drop to the ground [approx. 4-10 weeks after oviposition (USDA 1983)]. In either case, the insect chews an exit hole in the surface of the nut. Once out of the nut and on the ground, larvae bury themselves in a small cell where they spend the winter in diapause, emerging as adults after this time (USDA 1983, Manel and Debouzie 1997, Menu et al. 2000, Soula and Menu 2003). Diapause in this species begins in October (Menu and Debouzie 1993).

Most larvae pupate the following year but some of this cohort may pupate after 2-3 years (USDA 1983, Soula and Menu 2003). After one year in diapause, 59% of larvae emerge as adults, but less (37%) emerge after 2 years in an extended diapause; very few (4%) emerge after 3 years in the ground (Menu et al. 2000, Soula and Menu 2003).

Pupae Pupation typically begins in May but can start in August (USDA 1983). In France, pupation occurs in July and August with adult emergence occurring between August and the first part of October (Soula and Menu 2003). Pupation generally occurs outside of the nut in the soil (USDA 1983).

Interactions

Temperature

Environmental conditions during the pre-diapause period influence the length of the life cycle and whether or not diapause is induced (Manel and Debouzie 1997). Several studies describe developmental thresholds and accumulated degree days necessary for the completion of each phonological stage (Table D1). However, because of the complexity of the life-cycle, very few models have been developed to describe completion of the life-cycle development in response to temperature.

Table D1. Developmental threshold and degree day requirements for *Curculio elephas*

Stage	Developmental threshold (˚C)	Degree Days	Notes	Reference
Egg	6.5	108.9	Estimated under Natural conditions	(Manel and Debouzie 1997)
Larva	0	103 82 114 311 (for 1st 3 stages)	Stage 1 Stage 2 Stage 3 Stage 4	(Manel and Debouzie 1997)
	0	593	Median time for larval development	(Manel and Debouzie 1995)

Water

Drought conditions lead to hard-packed soils that inhibit the emergence of the adults from the ground (Menu 1993b, Soula and Menu 2003). In a summer drought, some females (approx. 27-87%) cannot emerge from dry, hard soil and therefore cannot reproduce (Menu 1993b).

Conversely, wet conditions can adversely affect populations. High soil moisture can increase mortality (Önuçar and Ulu 1989). Much of the mortality associated with moist soils may be attributed to microbial pathogens (See *Biotic factors* below). Rainy conditions can affect oviposition success (Debouzie et al. 2002).

Biotic Factors

Survival rates during the larval stage are generally low (Menu and Debouzie 1993). Predation from small animals (including millipedes), infection by pathogens, and hard or frozen soil (preventing larvae from forming pupation cells) contribute significantly to overall mortality rates (Menu and Debouzie 1993) (Soula and Menu 2003). Mortality is particularly affected during the prediapause stage when humans collect large numbers of chestnuts for consumption (Soula and Menu 2003). Parasite attack in *C. elephas* is minimal (Debouzie et al. 2002).