Biology, ecology and distribution of the Date Stone Beetle, *Coccotrypes dactyliperda* (Coleoptera: Curculionidae)

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This paper reviews the biology and ecology of the cryptic seed boring beetle *Coccotrypes dactyliperda*. Hibernating as an imago inside a seed, it can withstand mild winters, only to emerge in spring, spawning up to five generations during spring and summer. *Coccotrypes dactyliperda* is a comparatively long-lived Coleoptera species that has proven to be highly adaptable at infesting seeds of a wide range of palm species and thus was able to become naturalised in most subtropical and warm temperate environments.

**Keywords:** Life cycle; parthenogenesis; Date Palm; *Phoenix dactylifera*; arboricultural complex

**Introduction**

By their nature, cryptic arthropod species often go undetected and are less likely to attract the attention of ecologists, let alone the general public. This changes rapidly if and when they cause major economic or environmental losses. Among the bark and ambrosia beetles (Coleoptera: Curculionidae: Scolytinae), for example, much attention has been given to the ecological, and economic, impact of bark beetles that infest conifer forests (e.g. McNee, Wood, & Storer, 2000; Raffa & Berryman, 1983) as well as ambrosia beetles that inter alia cause fusarium dieback in commercial and ornamental palms (e.g. Eskalen et al., 2013; Hodel, 2017), especially when their outbreaks cause socio-political responses (Grégoire, Raffa, & Lindgren, 2015). Some of the species infest seeds and cause economic losses by spoiling fruit or preventing seeds from germinating successfully. One of these is the Date Stone Beetle *Coccotrypes dactyliperda*, which originated in the Middle East as part of the Date Palm (*Phoenix dactylifera*) arboricultural complex. Humans are the major vector unintentionally facilitating the species’ long-distance dispersal and ability to colonise new habitat across bodies of open water. Today it has become a truly cosmopolitan species throughout the warm temperate regions of the earth (Spennemann, 2019) due to its ability to accept the seeds of a wide range of palm species.

While the species causes substantial losses to the Date Palm industry due to fruit drop as well as spoilage of harvested drupes, it has gone largely undetected in most other settings as it only affects ornamental palms without causing a visually obvious damage that is readily recognisable by the wider public. To date the species has been subject to a number of experimental studies given its impact on the commercial Date Palm and palm nut industry, in particular in Egypt and Israel. Despite its global distribution and wide range of hosts, there is, to date, no comprehensive review of the biology of the species since Kirkendall (1993), in particular as it relates to its dispersal potential.

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and its ecological significance. This paper pulls together the disparate, global literature on the topic and will provide a comprehensive overview of the biology, ecology and distribution of the species.

The species

*Coccotrypes dactyliperda* (Fabricius, 1801) is a spermatophagus beetle of the Curculionidae beetle family (Coleoptera: Curculionidae; Scolytinae: Dryocoetini), with females measuring 1.9 to 2.2 mm in length and about 0.7 to 0.1 mm in width (Figure 1). Males are about two thirds of the size (Figure 2d–e). The beetle, which has a convex appearance and is hairy across the dorsal surface, ranges in colour from reddish-brown to almost black-brown (Schedl, 1961). The species was described in 1801 by Fabricius (1801) as *Bostrichus dactyliperda*, and as inhabiting date seeds (“habitat in dactylorum nucleis”). The species description was expanded by Letzner (1840) and Eichhoff (1879). The first formal observations of its breeding behaviour were made by Letzner (1840), who observed large quantities of beetles in single date seeds. Hornung (1842) was the first to document that the species also occurred in Betel Nuts (*Areca catechu*). From the 1850s onwards *Cocotrypes (Bostrichus) dactyliperda* was widely reported to occur during autumn in large numbers in date seeds in the inventories of pharmacies and fruit shops, primarily in southern Europe but also in temperate zones, destroying, or at least spoiling the stock with its excrement (Imhoff, 1856; Jäger, 1874; Nördlinger, 1855, 1869; Reitter, 1894; Vérardi & Joly, 1852).

**Life Cycle: Overview**

Female *Coccotrypes dactyliperda* bore into green dates (Ait-Oubahou & Yahia, 1999; Attia & Kamel, 1965; Kehat, Blumberg, & Greenberg, 1976), often near the funicle (Uyttenboogaart, 1927), causing the bulk of the affected drupes to abscise one to two days later (Blumberg, 2008; Blumberg & Kehat, 1982). Gómez Vives (2004) noted for the date plantations at Elche (Spain) that in many cases abscission was delayed however, and that the beetles developed in dates while still growing on the palm. The height of a palm does not seem to be related to the rate of infestation of green drupes. Observations by Hussein (1990) showed high variability between date varieties and no uniform trends. The species also predaes the seeds of fallen dates (Hussein, 1990), often after the pericarp has been eaten off by other animals, such as rodents.

*Coccotrypes dactyliperda* appears to exhibit food preferences for different date varieties. Among Egyptian date varieties, Hussein (1990) found that that green drupes of the Kakea and Soltani variety had a much higher infestation rate ($\bar{x}=6.18$ and 6.26 adults respectively) than drupes of the Saidi variety ($\bar{x}=1.26$). Similar observations were made, for other varieties (Aglawi preferred over Amri:Willcocks, 1914) as well as in India (Hillawi preferred over Khadrawi: Batra, 1972; Sohi & Batra, 1972). It appears that late season varieties such as Mejool, largely escape infestation (Sohi & Batra, 1972), which may be due to the fact that by that stage the beetles have ample fallen fruit to feed on (see below).

As with other crypto-parasites, the entire life cycle of *Coccotrypes dactyliperda* occurs inside the seed (Blumberg & Kehat, 1982) and by-and-large beetles only emerge when the food source is exhausted. When searching for new host locations, the species reacts to kairomones from date seeds, especially alcohol mediated fractions (El-Barbary, Donia, & Mostafa, 2002; Meisner, Weissenberg, Blumberg, & Ascher, 1985). Light does not seem to be a determining factor of emergence as in experimental settings no
statistically significant difference in emergence between simulated day or night could be observed (Spennemann, 2018a). While the species has been caught in a light trap in Israel (Schedl, 1969), it was noticeably absent in similar traps in other settings (Saudi Arabia: Al Dhafer & Alayeid, 2014).

After emergence from diapause, the first generation to leave the brood chamber emerges during late June/early July (in the northern hemisphere) and attacks the green drupes causing, what is colloquially known as the ‘July drop’ (Gómez Vives, 2004; Kehat et al., 1976). This continues until August, when a second generation emerges (Donia, El-Barbary, & Mostafa, 2002; Kehat et al., 1976). The rate of abscission varies, but when the infructescences are not protected from beetle attacks by chemical or physical (bags) means, production losses usually range between 20 and 40%. Reported have been losses of 17–22% in Punjab, India (Sohi & Batra, 1972), about 20% in Saudi Arabia and Egypt (Donia, et al., 2002), 25–40% in Bahria Oases, Egypt (Hussein, 1990), 25.5% in Israel (Kehat, Stoller, Meisner, & Greenberg, 1966); 30–40% Israel (Kehat, et al., 1976); 45% in Libya (Martin, 1959) and even 52.7% in Spain (Gómez Vives, 2004).

After initial attack, the fleshy part of the drupe is tunnelled through quickly, with the seed reached in less than an hour (El-Sufty & Helal, 1998). Over the following 24 hours an initial tunnel with a brood hole is excavated, which will then be enlarged continuously into a gallery. It has been argued that such galleries, from an evolutionary perspective are defendable resources (Kirkendall, Biedermann, & Jordal, 2015; Kirkendall, Kent, & Raffa, 1997). Indeed, when not laying eggs, tending the brood, or feeding, females tend to rest at not near the tunnel exit, effectively acting as a block.
Penetration of seeds by adult females is temperature and humidity dependent (Hussein, 1990), with the highest penetration rate around 28°C. Penetration rates decreased at both lower and higher temperatures (Salim, 1999). Indeed, in Israel the distribution of *C. s dactyliperda* seems to be correlated with humidity, as areas of low humidity (southern Jordan Valley and the Arava) appear devoid of the species (Bar-Shalom & Mendel, 2001; Kehat et al., 1976).

*Coccotrypes dactyliperda* are haplodiploid, which allows unmated females to lay eggs that produce male offspring and then to proceed to mate with these to produce offspring of mixed sex (arrhenotokous parthenogenesis) (Herfs, 1950). Consequently, the genus *Coccotrypes* has attracted the attention of geneticists as well as evolutionary biologists (Gottlieb et al., 2009; Gottlieb, Lubin, Bouskila, Gordon, & Harari, 2011; Holzman et al., 2009; Jordal, Normark, Farrell, & Kirkendall, 2002; Kirkendall et al., 2015). The hatched generations then continue to inbreed, effectively until the seed is exhausted. The ability of parthenogenetically producing males as well as continued sibling mating gives *Coccotrypes* is major advantage when colonising new sites and bioregions (Jordal, Beaver, & Kirkendall, 2001; Kirkendall, 1993).

Mated males may remain in the brood gallery, but run the risk of being killed by the female (El-Sufty & Helal, 1998). Male offspring of the female tend to be tolerated, presumably as they are need to fertilise the female offspring before their dispersal. The males are unable to excavate their own tunnels and galleries and rely on frass generated by the female (and later by the larvae for food) (El-Sufty & Helal, 1998).

Mated females start to lay eggs between one and three days after inhabiting a new seed (Herfs, 1950; Zchori-Fein, Borad, & Harari, 2006). Thereafter, the subsequent pre-oviposition period lasts between 3 and 13 days (Abd-Allah & Tadros, 1994; El-Sufty & Helal, 1998; Helal, 2014). Boraei, Khodeir, and El-Hawary (1994) observed that temperature (21°C vs. 25°C) caused no difference to the pre-oviposition period, but that it influenced the oviposition period, which was considerably longer at the warmer temperature (6–18 days at 25°C compared to 1–2 days at 21°C).

After oviposition, the female tends to remain in the brood chamber (Herfs, 1959) and tends the eggs to prevent fungal growth and keeps both the brood chamber and...
gallery clear of debris (Willcocks, 1914). All excreta generated by the larvae as well as frass are removed and expelled from the seed (Figure 3) (Herfs, 1950; Sitkov-Sharon, Tremmel, Bouskila, Lubin, & Harari, 2017). These actions seem to be shared among mothers and daughters when multiple generations are present in one seed (Herfs, 1948). It has been argued that keeping brood galleries free of frass contributes to ventilation and also nest hygiene, i.e. a removal of substrate for pathogens and parasites (Kirkendall et al., 2015).

When not tending the gallery, the female acts as a block, sitting at or near the tunnel entrance, thereby preventing larvae from falling out of the seed as such larvae are unable to excavate their own gallery and thus will perish (Biedermann & Taborsky, 2011; El-Sufty & Helal, 1998; Herfs, 1950, 1958; Van Der Merwe, 1923) (Figure 4). If a blocking mother is removed, and there is no daughter to take her place, the brood chamber may be occupied by another female. In such an instance the new female tends to clear the chamber of its predecessor’s eggs and commence its own breeding (Herfs, 1948, 1950).

The size of the total brood and the number of generations that can be reared in a single seed is determined by the time of the year of the initial infestation and the physical size of the seed.

**Brood Sizes**

**Date Palm (Phoenix dactylifera).** A single date seed can concurrently house large numbers of eggs, larvae, pupae and imagines. Letzner (1840), who was the first to observe large quantities of beetles in single date seeds, also noted that the larvae were of different sizes, which indicated that there were either multiple generations or multiple broods in the same seed.

An average number of 3.4±0.9 eggs was oviposited daily and these eggs were accumulated as clusters in the seed (Aly 1995; Zchori-Fein, et al., 2006). Oviposition will occur for at least 17 days inside a seed (Zchori-Fein et al., 2006), but possibly even longer, with a female producing on average 30 offspring (Blumberg, 2008). The numbers range from 12–15 adults found in imported seeds in the Rhineland of Germany.
Figure 4. Longitudinal cross-section of an infested seed. The seed contained 87 Coccotrypes dactyliperda in various stages of development. Note the female blocking the exit to the brood chamber. – From: Spennemann et al. (2018).

(Bach, 1854), 15 larvae and adults reported from Greece (Vassilaina-Alexopoulou, Mourikis, & Buchelos, 1986), 26 eggs found in seeds in South Africa (Van Der Merwe, 1923), one female, 4 pupae, 23 larvae and 20 ova in an affected seed observed in Egypt (Willcocks, 1914), and 40–60 eggs detected in seeds imported from Tunisia to France (Dechaux, 1890). Letzner (1840) noted one seed with 10 larvae, 8 pupae and 30 adults, and another seed with 78 larvae, 5 pupae and 17 adults. Other studies reported 50 adults Coccotrypes dactyliperda in Israel (Gottlieb et al., 2009), 60±10 adults in Italy (Longo, Russo, & Palmieri, 1991); 50–70 adults in Algeria (Doumandji-Mitiche, 1977). Depending on its size, a single seed may supply resources for three overlapping generations (Sitkov-Sharon et al., 2017).

Canary Island Date Palm (Phoenix canariensis). In September 1927, Swezey (1928) collected 38 seeds (all with a single hole) at Kapiolani Park in Honolulu, Hawai’i. Between 25 October and 3 November a total of 3,518 individuals emerged, giving an average of 92.6 individuals per seed.

Dissecting infested Phoenix canariensis seeds during a germination experiment in Australia, working with single seeds (rather than relocated females), Spennemann et al. (2018) noted from 55 to 87 individuals of all stages. In a food preference experiment a total progeny of 37.8±26.2 (median 35, range 6–93) (n=46) adults were observed which derived from single seeds (Spennemann, 2018a). The substantial range was due to varied humidity conditions and infestation with mould, highlighting environmental variables that are central to the reproductive success.

Dum Palm (Hyphaene thebaica). Dum (doum) palms produce drupes with comparatively large nuts, which measure 45–50 mm in length and about 35–40 mm in diameter. Given the large size, 600–1300 beetles have been reported as emerging from individual seeds (Roonwal, 1971). Roonwal (1971) examined the infestation of dum nuts and products made from these in Southern India. In his observations 18,655 individuals emerged from a supply of 55 whole nuts, 142 pieces and 118 buttons. Herfs (1958) noted 4,408 adults, pupae larvae and eggs in a single dum nut of 40.2 g weight (72% of which have been consumed).

Tagua (Phytelephas sp.). Herfs (1948) experimented with complete tagua / corizo seeds (Phytelephas sp). Five seeds produced in total 2,944 females and 445 males, whereas a 10 large, processed buttons produced 155 females and 42 males.

Other palms. In Nephrosperma vanhoutteana brood sizes of 5–40 individuals (x=23.4, n=10) have been reported (Beaver, 1987).
Total fertility
The total number of offspring produced by females was ascertained by Herfs (1950), who extracted fertilised females from their gallery after 23 days, counted the offspring and allowed it to establish a fresh gallery. He noted that females established on average three broods (range 2–5, n=22) (‘generations’ in Herfs), with an average total number of 93.9±24.7 (range 40–144, n=22) offspring. The average number of offspring steadily decreased from brood to brood (from 36.7 in the first brood to 9 in the fifth brood). In a separate experiment, non-fertilised females were extracted after oviposition and allowed to establish a fresh gallery. These females had on average 6 broods (range 1 to 11, n=24), with average 21.2±12.2 (range 3–56, n=24) offspring. El-Sufty and Helal (1998), who carried out similar experiments on *Phoenix dactylifera* in Egypt, obtained a total progeny of 37.4±7.7 (range 26–48).

Development period of a full life cycle
Experimental studies showed that temperature plays a major role in the speed of development of *C. dactyliperda* (Blumberg & Kehat, 1982; Boraei, et al., 1994). The threshold temperature for development appears to be 12.3°C (Blumberg, 2008). Experimental studies by Blumberg and Kehat (1982) showed that at 28°C and 70% relative humidity the average egg development period was approximately 6 days, followed by 12–15 days of the larval stage (three instars), and 4 days of the pupal stage. Boraei et al. (1994) tested the response of *C. dactyliperda* at temperatures of 21°C and 25°C (at 60–70% humidity) and found that the egg development period was 7-10 days at 21°C but only 4–6 days at 25°C, followed by 20–23 days (11–19 at 25°C) for the larval stage and 6–13 days (4–10) at the pupal stage. This was followed by an immature imago stage in the seed, that took 37–44 days at 21°C and only 20–34 days at 25°C (Boraei et al., 1994).

The development period of a full life cycle from egg to adult for females is reported as 20 days in summer (Boraei, 1994), 22 to 29 days in summer in India (Nair & Oommen, 1968), three weeks at 30°C and nine weeks at 20°C (Herfs, 1959); 22.2 days at 28°C and 30.2 days at 25°C (Salim, 1999); 24.8 days (males 22.1) (Blumberg & Kehat, 1982); 28–30 days in summer and 69 days in winter for South Africa (Van Der Merwe, 1923), one month in summer and two in winter for Australia (Froggatt, 1935) (Figure 5).

Not taking into account the effects of seasons, there appears to be substantial variation in the egg development period between the generations, but no clear patterns emerge (Abd-Allah & Tadros, 1994; Aly, 1995). In a given year, when feeding on *Phoenix dactylifera* seed, between five and six generations can be expected, with up to eight generations on record (Bar-Shalom & Mendel, 2001; Boraei, 1994). The same can be assumed for palms with similar-sized seed and similar fruit drop patterns (e.g. *P. canariensis*). There are, at present, no data on the number of generations in the seeds of other host plants (see below). It can be surmised that larger seeds, such as dum or tagua/corizo provide a greater volume of albumen and thus allow for a greater number of broods and generations to feed. This aspect, however, warrants further research as it impacts on the ability of *Coccotrypes dactyliperda* to establish itself in new areas.

Diapause
During the winter period imagines of female *Coccotrypes dactyliperda* enter a diapause or dormancy period (in some sources labelled ‘hibernation’). It was first alluded to by Del Guercio (1919) in his work on the beetle’s impact on dum palms (*Hyphaene thebaica*) in the Italian colonies in Africa.
Figure 5. Development period of a full life cycle from egg to adult for females (in days) as a dependent of temperature. See Supplementary Table S1 for data.

First generation imagines tend to spend the cooler winter period inside the *Phoenix dactylifera* seed in which they hatched, in the northern hemisphere usually from November or December to February (El-Bahria Oasis, Egypt: Ali, Metwally, & Hussain, 2003) or even as long as until May (Abd-Allah & Tadros, 1994; Helal, 2014). The commencement and termination of diapause were linked to both temperature and photoperiods. In the Middle East, temperatures at or below 15°C coupled with reduced photoperiods (short days) seem to initiate diapause, while temperatures above 25°C and longer photoperiods terminated diapause. Boraei (1994) noted that even in cooler temperatures artificially extended photo periods (17 hours light, 7 hours darkness) resulted in higher activity and even oviposition. Similar diapause patterns have been observed among *C. dactyliperda* living in dum nuts in Uttarakhand, India (Roonwal, 1971), with mass emergence in late April and May.

Diapause of *C. dactyliperda* cannot be solely linked to temperature and photoperiod triggers, however, as diapause is also reported from at locations, where both the temperature and photo period regime are less varied. Roonwal (1971) observed diapause among specimens bred in Tamil Nadu (Southern India) with mass emergences in March. At Chennai temperatures do not drop below 21°C and the summer and winter photo periods vary only by 1.5 hours (compared to 4.5 hours in Egypt). This aspect warrants further investigation, as it impacts on the detectability of the species in the field.

**Life expectancy**

The longevity of the female beetle is influenced by temperature and the commencement of diapause (Boraei et al., 1994). The average mated female has a life expectancy of 63 days, while unmated females lived on average 10 days longer (Blumberg & Kehat, 1982). Other sources suggest that females can be even longer lived (~90 days) with a generation time of ~25 days (Gottlieb et al., 2011). Herfs (1950) showed that the life expectancy of breeding females was highly variable, with an average of 98.9±34.9 days (range 50–174 days) at 25°C. An unfertilised female lived for 256 days, laying ten gen-
erations of eggs, with second individual living for 194 days, laying nine generations of eggs (the females were extracted just after oviposition preventing fertilisation by their offspring). Males lived up to 187 days (all at 25°C) (Herfs, 1950).

The life expectancy of starving / non-feeding individuals influences their ability to disperse into areas of low food density. Herfs (1950) found that without food freshly hatched females on average survived for 9.9 days (range 4–31), while males lasted for 8.5 days (range 2–20).

**Cold Stress and Heat Stress**

While low temperatures initiate diapause, temperatures, as well as high temperatures and low humidity cause mortality. The life expectancy of females was a low as 2.1 days at 35°C with 40% humidity (Salim, 1999). It is not clear, however, how long the exposure was at these temperatures. As early as 1840 it was noted that the development of *C. dactyliperda* slowed in cooler, but non-freezing temperatures. In Wrocław, Letzner (1840) also observed total mortality among Date Stone Beetles that were exposed to environments during late November 1839 where average ambient temperatures were 6.1°C (Bryś & Bryś, 2010).

*Coccotrypes dactyliperda* are able to withstand sub-zero temperatures for short periods of time, in particular when in the brood chamber inside the seed which buffers the temperature. In North Africa and the Middle East temperatures can drop to sub-zero temperatures such as -1.7°C (Tripoli, Libya), -4.0°C (Jerusalem), -6.1°C (Tunis) and -8.0°C (Amman). In the south of France, where *C. dactyliperda* has become naturalised, temperatures can drop to -13.0°C (Toulon) (see https://www7.ncdc.noaa.gov/CDO/cdo). When experimentally exposed to an ambient temperature of -8°C, unprotected *C. dactyliperda* survived for 75 min, with 72% still alive after 3 hours (full mortality at 4 hours). Beetles in their galleries started to die after 2.5 hrs exposure, but 20% remained alive after 7 hrs (Spennemann, unpubl.).

**Host species**

Seed borers of the genus *Coccotrypes* are known to affect a range of plants (Wood & Bright, 1992) such as palms by *Coccotrypes dactyliperda* (Supplementary Table S2), *C. palmarum* (Allmen, Morellato, & Pizo, 2004) and *C. carpophagus* (Bright, 1987). Other affected species are as diverse as seeds of *Quercus* spp. and *Lithocarpus edulis* (Acorn Borer, *C. graniceps*) (Nakamura et al., 2013; Ueda, Fujita, & Urano, 2001) and even the propagules of some mangroves *Rhizophora mangle* (*Coccotrypes rhizophorae*) (Martínez-Zacarías et al., 2017). An important characteristic is that *Coccotrypes* sp. are highly adaptable and are able to broaden their host spectrum.

In its endemic range, the original host of *C. dactyliperda* was the Date Palm (Blumberg & Kehat, 1982; Vassilaina-Alexopoulos et al., 1986; Zchori-Fein et al., 2006), a claim which seems to be supported by archaeological evidence (see above). With the spread of ornamental horticulture and the concomitant, increasingly global dispersal of Canary Island Date Palm seeds and seedlings (Spennemann, 2018b; Zona, 2008) as well as dates for human consumption (Terral et al., 2012), *C. dactyliperda* has spread to numerous countries across the globe (see below) where it was able to adapt to a range of other hosts. Today, *C. dactyliperda* breeds in virtually all tropical and subtropical, as well as many warm temperate areas of the world.

The beetles broadened their host range to many palm species in general (Supplementary Table S2) as well as palm seed products such as buttons made from dum nuts.
(Hyphene thebaica) and tagua (various Phytelephas species, primarily Phytelephas macrocarpa). In addition, the beetle has been documented as breeding almonds (Prunus dulcis), as well as pasta residues. Based on a review of published observations as well studies, under studies under laboratory conditions seeds of a number of other species have been reported as infested with the beetles, but it is not clear whether these beetle populations were breeding or merely surviving on a maintenance diet. Other seeds were rejected outright (for references see Supplementary Table S2). It appears that hard- and thick-shelled seed, such as apricot, olive or walnut were rejected whereas thin-shelled seed such as chestnuts and hazelnuts were at least tested by tunnelling.

Distribution

Based on sub-fossil evidence obtained from archaeological sites, the origin of C. dactyliperda lies somewhere in the Middle East and was associated with the Date Palm complex. Carbonised or otherwise preserved subfossil remains of C. dactyliperda have been recovered from bronze age (2200-2500 BCE) sites in Oman (Costantini & Audisio, 2000), the Amarna Period (c. 1350 BCE) in Egypt (Panagiotakopulu, 2001), and 100 BCE – 150 CE sites in Israel (Kislev, 1992; Simchoni & Kislev, 2009). During Phoenician and Roman times it spread along the Mediterranean coast of North Africa. By late Medieval times it had become established in the south of France (Ponel, Andrieu-Ponel, & Bouiron, 2014), from where it was distributed globally primarily through the horticulturally derived dispersal of one of its adopted host species, Phoenix canariensis (Spennemann, in prep). During the late 19th and early 20th centuries, C. dactyliperda continued to arrive in Europe in shipments of dates from the Middle East and Africa, betel nut from the East Indies and vegetable ivory (for buttons) from East and North Africa, as well as Ecuador, and was encountered in stores of wholesalers and merchants (Eichhoff, 1881, 1890; Hagedorn, 1904) where it readily acclimatised in climate-controlled environments (Pax, 1921).

Today the species has a global distribution in subtropical and warm temperate climes (Figure 6). Given that the underlying data have been drawn from a wide range of sources (Spennemann, unpubl.), there is possible taxonomic uncertainty to some identification. This, however, does not dramatically bias the general picture. Classified as ‘naturalised’ are observations where C. dactyliperda has established breeding populations outside its endemic range and in the natural environment. Classified as ‘introduced’ are observations where C. dactyliperda has been recorded as arriving in a given country, but where the beetles cannot establish breeding populations outside environmentally controlled environments (such as laboratories, greenhouses of nurseries and store/warehouse houses).

Coccotrypes dactyliperda is a pest species that is readily dispersed with modern trade and is frequently intercepted in shipments (Brockerhoff, Bain, Kimberley, & Knizek, 2006; Haack, 2001) with population movements crisscrossing the globe. If interception data from the U.S.A. are any guide, then we have to expect multiple importations of C. dactyliperda from various countries. According to the data of the Bureau of Entomology and Plant Quarantine (full references given in the Supplementary Material), the species was found in the 1930s in shipments of plants and plant products, as well as personal luggage arriving from France, Germany, India, Italy, Liberia, Mexico and Tunisia, and during the 1940s from Algeria, Costa Rica, Ecuador, France, Iraq, Mexico, New Zealand, Panama, Portugal, Trinidad, Tunisia, and Turkey (Figure 7).
Ecological considerations

Widely regarded as an agricultural pest, its ecological significance is not very well understood. Very little is known about the ecology of the species in its endemic range as part of the Date Palm arboricultural complex in the Middle East; the secondary palm nut habitats in South America (Phytelephas sp.) or Northern and Eastern Africa (Hyphaene thebaica), or in urban parklands among Phoenix canariensis.

Given its ability to infest a range of host plants, the species has been declared a quarantine species of which imports are prohibited in a number of countries, such as the then USSR (Oakley, 1940) or Syria (even though its existence in a naturalised state is highly likely) (according to a Government Decree No. 60/T of 14.02.2009). Its nature
as a pest infesting Date Palm plantations has led to a number of studies on the control, or at least management of the pest in the Middle East (Ali, Metwally, & Hussain, 2002; Ali et al., 2003; Anber, Helal, & El-Sufty, 1998; Helal, 1998; Mostafa, 1997) and India (Batra, 1972) but also by the button industry in Ecuador and elsewhere (Tewari, 1954; van der Merwe, 1923). In commercial Date Palm plantations, the bagging of infructescences with cloth of sub-1 mm mesh size has proven the most effective against various insect species, including *C. dactyliperda*.

The beetle species was also identified as a potential museum pest in Egypt and similar areas which might affect date and dum palm collections, as well as objects made from seeds of these palms (Krajewski, 1999). Experimentation has shown, however, that old, dried-out and hardened tagua (*Phytelephas* spp.) buttons were uniformly rejected, while fresh button blanks, as well new buttons (softened by soaking in water) were accepted (Spennemann, 2018a).

Some studies of *Coccotrypes* species have shown that the beetles can cause severe degradation of the seedbank and thus reduce the reproductive success of some plant species unless seeds were buried by seed-caching vertebrates (Kuprewicz, 2015). Documented are the impacts of *Coccotrypes palmarum* on *Euterpe edulis* (von Allmen et al., 2004) and of *Coccotrypes rhizophorae* on the propagules of *Rhizophora mangle* (Martínez-Zacarías et al., 2017).

Only limited data exist for the ecological effects of *C. dactyliperda*. A study in Israel found that Date Stone Beetles were responsible for about 20% of the of the annual seed bank due to feeding induced abscission (Bar-Shalom & Mendel, 2001). At the end of the breeding season in October, some 10% of the seeds on the ground were colonized, but after diapause and the first generation in March, 95% of the seeds on the ground showed evidence of infestation (Bar-Shalom & Mendel, 2001).

Experimental data have shown that the numerous seeds impacted by *C. dactyliperda* germinated although they had been penetrated (Spennemann et al., 2018). This suggests that the location of the penetration is of significance. Seeds where the embryo was affected by initial tunnelling failed to germinate, while the others did. The progressive consumption of the seed’s albumen by the beetle, however, implies that the emerging epicotyl has less energy at its disposal, and thus is likely to wilt before it can form viable rootlets and a photosynthetically active leaflet.

**Dispersal**

**Self-aided dispersal of *Coccotrypes dactyliperda***. The primary dispersal of *C. dactyliperda* is self-aided, whereby emerging females will seek a new host seed. In spring, after emergence from diapause, the females will move into the crown of the palms and bore into a green drupe (see above). Experimental observations showed that the beetle would infest drupes growing up to a height of 5-7m (Hussein, 1990), with 8 m being regarded at the edge of capacity. Thereafter, the beetles tend to infest both drupes on the tree and fallen drupes and seed on the ground. El-Sufty and Helal (1998) assert that the beetles prefer to crawl up the stem of the palm and then along the inflorescence to reach the drupes rather than to fly. Observations made during a germination experiment showed that *C. dactyliperda* readily took flight even though other seeds were nearby (Spennemann et al., 2018). This may suggest short-distance dispersal is favoured over exploration of the immediate surroundings, in particular in situations with a high beetle density. Indeed, El-Sufty and Helal (1998) observed that flight might be initiated in crowded conditions.
There are only limited very limited observational data on the vertical and horizontal flight capacity of *C. dactyliperda*. While El-Sufty and Helal (1998) note that (under laboratory conditions) flight would be a short distance (‘a few centimetres’) only horizontal flight/dispersal distances of ~50m have been documented under field conditions (*Coccotrypes* sp. in Colombia; Ramirez, Parrado-Rosselli, & Stevenson, 2009).

Experiments with similar sized bark beetles can inform on the flight capacity of *C. dactyliperda* as there are no biomechanical reasons that like-sized scolytid beetles should perform substantively different. Bark and ambrosia beetles fly at speeds less than 1 m/sec (Menocal, Kendra, Montgomery, Crane, & Carrillo, 2018). In laboratory experiments, for example, walnut twig beetles (*Pityophthorus juglandis*), flew on average 158 m with maximum single flight of 1.2 km. A maximum total flight distance of 3.6 km in a 24 hr was observed (Kees, Hefty, Venette, Seybold, & Aukema, 2017).

**Vector-aided dispersal.** Vectors responsible for the spread of the beetles have not been studied in any detail. Setting aside human assisted dispersal (see above), the major vectors are wind-dispersal as well as dispersal by vertebrates.

Vertebrates feeding on seeds, such as rodents, can be ruled out as they will destroy the brood chamber and thus effectively terminate propagation. Numerous terrestrial and volant vertebrates, which ingest ripe or fallen *Phoenix dactylifera* and *P. canariensis* drupes, act as vectors for the dispersal of the seeds (Spennemann, 2018c, 2018d), and thus also of beetles that are infesting them. The infested seed may either be exposed to mastication and subsequent ejection from the oral cavity (e.g. fruit bats; Spennemann, 2018c); to partial digestion and subsequent regurgitation from the crop (e.g currawong; Spennemann, unpubl.); or to partial digestion and subsequent defecation (e.g. canids). The survival of a female and her brood will depend on the duration of exposure to gastro-intestinal liquids (saliva, gastric acid etc.) during gastro-intestinal transit as well as the nature of ingestion and duration of mastication (if any). No experimental data exist that shed light on the survivability of *C. dactyliperda* in such situations.

Golden Jackals (*Canis aureus*) are widely reported to feed on fallen dates of *Phoenix dactylifera* (Spennemann, 2018d) and other palms. The ingestion of infested *Chamerops humilis* seeds by Golden Jackals was reputedly not detrimental to the survival of beetles or their larvae (Lucas in Anonymous, 1846; Lucas, 1849) despite the potential long gastro-intestinal transit times. Golden Jackals have a linear home range of 0.5 to 12 km and their habitats include fragmented peri-urban landscapes and date plantations, where they, like other canids, mark their territories with scats, thereby dispersing *C. dactyliperda* infested seeds.

Wind-dispersal can easily carry the light-weight beetle (on average 1.25 mg) over long distances. While the horizontal and vertical movement (by flight) of wind-deposited females may be limited to a range of 1 km or less, the relative longevity of female *C. dactyliperda* even without food (on average 9.9 days at 25°C, see above) suggests that the beetles have a high probability of locating new food source if they exist near their drop zones. As noted earlier, when searching for new host locations, the species reacts to kairomones from date seeds, especially alcohol mediated fractions (El-Barbary et al., 2002; Meisner, et al., 1985).

**Natural predators and parasites**

Given its cryptic nature, comparatively little is known about the natural enemies of *C. dactyliperda*. Ecological assessments in Algeria have shown that the beetle is predated by the Bulbul (*Pycnonotus barbatus*) (Milla, Doumandji, Voisin, & Baziz, 2005), the
Common Blackbird (*Turdus merula*) (Salima & Salaheddine, 2014), the Spotted Flycatcher (*Muscicapa striata*) (Boukhemza-Zemmouri, Belhamra, Boukhemza, Doumandji, & Voisin, 2011) and in particular by the European Robin (*Erithacus rubecula*) which relies on *C. dactyliperda* as food during winter (Smaï et al., 2014) and the House Martin (*Delichon urbicum*). *Coccotrypes dactyliperda* was noted in 20.8% of scats (Abdelghani, 2011).

The beetles are known to be hosts to *Androlaelaps* sp. mites, which were found riding on the beetles between the pronotum and the thorax (El-Kaws & Negm, 2018; Ibrahim, Abdel Samad, & El-Gazzaar, 1992). A beneficial role may be played by *Rickettsia* bacteriae which were detected among some *C. dactyliperda*. It has been surmised that they are likely to be associated with oocyte maturation, parthenogenesis induction, host feminization and the killing of males (Merhej, Angelakis, Socolovschi, & Raoult, 2014).

**Avenues for future research**

While *C. dactyliperda* has proved to be a highly adaptable species that can feed and breed in a range of palm seeds, its food references and breeding habits have only been examined for a few palm species. Given the significance of the species as a pest in commercial Date Palms, as well as in dum and tagua nut buttons, feeding experiments have been limited to those species. In the latter case, infestation of nuts seems to occur after harvest, with beetles able to propagate multi-generationally in storehouses. The role of other seeds as food sources for *C. dactyliperda* is much less well understood. For example, the prolonged availability of large quantities of seeds of *Phoenix dactylifera* and *P. canariensis* allows the species to annually produce multiple generations of offspring in successive seeds, with the last generation finding a fresh seed to spend their diapause. It is unclear, however, how such multigenerational breeding can be achieved in other species that do not exhibit the seasonally near continuous fruit drop common among some palm species. Finally, there is space for in-depth research into the ecological significance of *C. dactyliperda* and its impact on the seedbank and thus the reproductive capacity of the various host species.

**Supplementary Material**

Supplementary Material is available via the “Supplementary” tab on the article’s online page (http://dx.doi.org/10.1080/09397140.2019.1571743).

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