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Observations of seed penetration action by the date stone beetle *Coccotrypes dactyliperda* (Coleoptera, Curculionidae, Scolytinae)

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ABSTRACT. Date stone beetles (*Coccotrypes dactyliperda* Fabricius, 1801) tunnel into palm seeds to establish brood galleries with their larvae consuming the seed's albumen. Based on behavioural observations this paper describes the biomechanical parameters that govern the initial excavation of the tunnels and the establishment of the brood galleries.

Key words: Spermatophagy, feeding behaviour, locomotion, activity patterns

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Introduction

The date stone beetle, *Coccotrypes dactyliperda* (Fabricius, 1801), is a cryptic spermatophagus beetle (Coleoptera: Curculionidae: Scolytinae: Dryocoetini), with females measuring 1.9–2.2 mm in length and about 0.7 to 1 mm in width. 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, Fabricius, 1801, Letzner, 1840, Eichhoff, 1879). The entire life cycle of *C. dactyliperda* occurs inside the seed (Blumberg & Kehat, 1982). Initially distributed in the Middle East and North Africa as part of the date palm horticultural complex, the distribution range of the species has seen a remarkable increase during the nineteenth century, mainly due to the trade in dates as fruit for human consumption; the distribution of palm seeds (in particular *P. canariensis*) for horticultural endeavours; and in the form of vegetable ivory for button manufacture. Today, *C. dactyliperda* has become a true cosmopolitan species that can be found in most subtropical and temperate zones (Spennemann, 2018b). The beetle attacks the green drupes of the date palm (*Phoenix dactylifera* L.), causing the bulk of these to abscise one to two days later (Blumberg, 2008) with production losses between 20 and 40% (Hussein, 1990, Kehat et al., 1976). The species also predated the seeds of fallen dates, often after the pericarp has been consumed by other animals, such as rodents. *Coccotrypes dactyliperda* also attack other palms, in particular the Canary Island date palm (*Phoenix canariensis* Chabaud, 1882) (for review of the beetle species see Spennemann, 2019a).

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Given that the behaviour of the species is primarily cryptic, it is of little surprise that there are only very few published observations that examine the tunnelling behaviour of the species. On record are only two papers by Adolf Herfs (1948, 1950) who primarily commented on factors such as hardness of seeds and traction.

An opportunity for further observations arose when quantities of beetles were needed for a series of experiments assessing food choices and emergence times of *C. dactyliperda* (Spennemann, 2018a) as well as a range of experiments assessing the resilience of *C. dactyliperda* when exposed to subzero temperature, digestive fluids and insecticides (Spennemann, 2020a, 2019b, 2020c, Spennemann et al., 2018). The experimental parameters of these studies required that the beetles had commenced to established galleries inside *P. canariensis* seeds. Observations showed that *C. dactyliperda* were not readily disturbed once they had commenced tunnelling to a level that their eyes were below the seed's surface. This provided a unique opportunity to collect observational data to document the tunnelling process in more detail. This paper will report on these observations and examine the nature of tunnelling into seeds.

Material and methods

The *Coccotrypes dactyliperda* beetles used in this experiment were drawn from a population raised at the PC2 laboratory of the Peter Till Laboratories, Faculty of Science, Charles Sturt University (Albury, Australia). The population had initially been bred for use in a multi-factorial experiment, assessing food choices and emergence times (Spennemann, 2018a). The original beetle population stemmed from *Phoenix canariensis* seeds collected under a single palm at Alma Park, NSW, Australia (Spennemann et al., 2018, Spennemann, 2020a). During the assessment of food choices (Spennemann, 2018a), individual *C. dactyliperda* specimens were exposed to food options in clear 200 ml plastic sample jars, where they could be observed exploring and tunnelling into seeds. Three samples, where tunnelling was in progress, were extracted from the jars and their tunnelling action video-recorded. A fourth observational sample was obtained during sample preparation for an experiment to assess whether *C. dactyliperda* would infest vertebrate-defecated palm seeds (Spennemann, 2020b).

Four samples, where tunnelling was in process, were placed in front of a camera (Olympus TG-3 camera set to 'microscope' macro) and the tunnelling efforts were video-recorded. The subsequent footage was viewed, analysed and the activity of the beetle encoded as gnawing (G), debris removal (DR) and pauses (P). Movement was recorded as clockwise (CW) and counter-clockwise (CCW). The direction of the camera was arbitrarily coded as 'N' and the orientation of the beetle's pronotum in relation to the camera direction expressed as octants of the cardinal directions (i.e. N, NE, E, SE etc.). The footage was shot either hand-held or tripod mounted. In total 6 hours and 53 minutes of footage were collected recording four different penetration events. These were penetrations to *Phoenix canariensis* (6:14:03 h recorded, 2:21:18 h analysed); *Corylus avellana* (Figs 1, 3) (20:57 min); *Washingtonia robusta* (Fig. 2) (14:28 min); and a blank for a Tagua button (*Phytelephas macrocarpa*) (3:26 min) (Table 1). The data sets were compared using the ANOVA function of R (Gentleman, 2008), using Dunn's (1964) Kruskal-Wallis multiple comparison (*p*-values adjusted with the Benjamini-Hochberg method). Pairwise comparisons used student's *t*.

Table 1. Documented activities (hh:mm:ss).

Sample	Hardness	Tunnelling	Debris Removal	Pause	wriggles legs	Total
<i>Corylus avellana</i>	hard	00:13:53	00:01:20	00:05:42	00:00:02	00:20:57
<i>Washingtonia robusta</i>	medium	00:13:14	00:01:14	-	-	00:14:28
Tagua button blank	very hard	00:03:26	-	-	-	00:03:26
<i>Phoenix canariensis</i>	soft	01:39:38	00:41:40:	-	-	02:21:18

**Figure 1.** Penetration attempt to a hazelnut (AG5) (not video-recorded).

Results

Coccotrypes dactyliperda beetles were observed chewing into the epicarp in a circular fashion by frequently repositioning themselves in approximately one-eighth to one-quarter turns (Figs 2, 3). This repositioning can occur clockwise or counter-clockwise, with changes in direction occurring in the same gnawing sequence (*i.e.* beetles did not always turn into the same direction). The four recorded penetration events demonstrate the behaviour of the beetles, but also highlight differences based on the nature of the seeds to be tunnelled.

Beetles were observed to frequently repositioning themselves by clockwise or counter-clockwise quarter-turns. To test, whether the duration of gnawing action between turns was influenced by the hardness of the seed, the average duration of tunnelling events was computed. There appears to be a congruence, with beetles repositioning themselves at shorter intervals in the hard seeds, with much longer intervals in the softer seed (Table 2). The duration among soft seeds is significantly longer ($p < 0.001$) than all others. The duration of tunnelling events into very hard tagua button blanks were significantly shorter ($p = 0.04$) than *Washingtonia robusta* seeds (Table 3).

Table 2. Average duration of events between turns (mm:ss).

Sample	Hardness	Tunneling events			Debris removal events		
		Mean \pm SD	min-max	<i>n</i>	Mean \pm SD	min-max	<i>n</i>
<i>Corylus avellana</i>	hard	00:19 \pm 00:25	00:02-02:23	43	00:40 \pm 00:35	00:15-01:05	2
<i>Washingtonia robusta</i>	medium	00:29 \pm 00:30	00:01-01:40	27	00:11 \pm 00:10	00:03-00:30	7
<i>Tagua</i> button blank	very hard	00:09 \pm 00:15	00:02-01:18	23	-	-	-
<i>Phoenix canariensis</i>	soft	02:02 \pm 01:44	00:03-06:33	49	00:53 \pm 01:12	00:03-00:05:42	47

Table 3. Differences in average duration of tunnelling events (*p* values given).

Sample	Tunneling events				Debris removal events		
	<i>Corylus</i>	<i>Washingtonia</i>	<i>Tagua</i>	<i>Phoenix</i>	<i>Corylus</i>	<i>Washingtonia</i>	<i>Phoenix</i>
<i>Corylus</i>	-	0.620	0.062	0.000	-	0.177	0.844
<i>Washingtonia</i>	-	-	0.040	0.000	-	-	0.018
<i>Tagua</i>	-	-	-	0.000	-	-	0
<i>Phoenix</i>	-	-	-	-	-	-	-

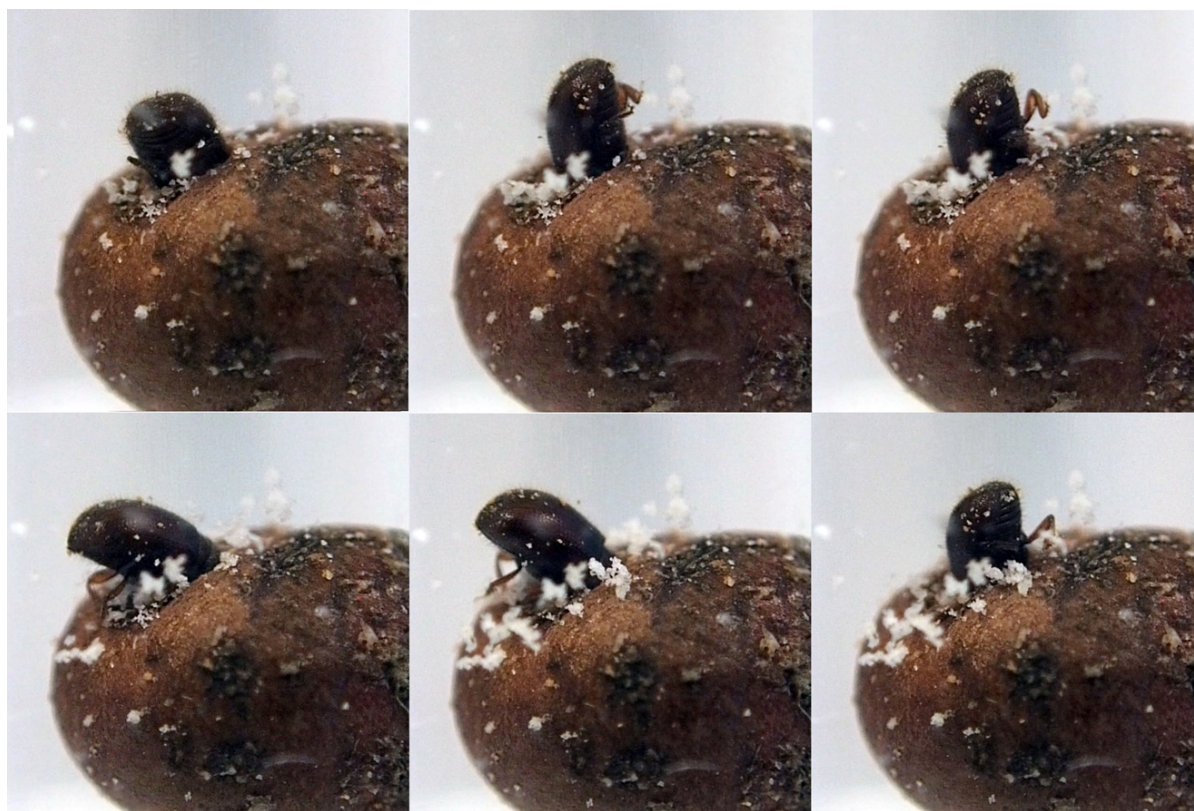
**Figure 2.** Tunnelling sequence into *Washingtonia robusta*.

Table 4. Proportions of directional turns (in %).

Sample	Hardness	Counter-clockwise	Clockwise	No change	<i>n</i>
<i>Corylus avellana</i>	hard	31.8	47.7	20.5	44
<i>Washingtonia robusta</i>	medium	78.6	17.9	3.6	28
Tagua button blank	very hard	16.7	79.2	4.2	24
<i>Phoenix canariensis</i>	soft	50.0	50.0	0.0	70

**Figure 3.** Abandoned penetration attempt into *Corylus avellana*. Stills from a video.

Clearly, it can be posited that harder seeds will produce less debris ('frass') than soft seeds for the same duration of gnawing. While this is well illustrated in the relative frequency of debris removal events, it does not translate into the average duration of the events (Table 2). On average, beetles took significantly longer expelling frass from the tunnels drilled into *Phoenix canariensis* seeds compared those dug to *Washingtonia robusta* ($P=0.018$). The times used in other combinations were not significantly different (Table 3). While there are observable differences between the frequency of clock-wise and counter-clockwise turns in each of the samples, no a clear pattern emerges, for example between hard and soft seeds (Table 4). Based on the confidence limits for the proportions set out in Table 4, the observed differences in direction at significant $p<0.001$ for *Washingtonia robusta* and for the Tagua button blank (University of California, 2019). Considering the average duration of clock-wise and counter-clockwise tunnelling events, differences are observable (counter-clockwise events taking longer), but these differences are not significant (Table 5). The hardness of the penetrated material has direct influence on the amount of debris that is generated in a set time and therefore influences the time intervals between debris removal. A date stone beetle penetrating into a *Washingtonia robusta* seed (Fig. 3), for example, tunnelled for variable intervals (4:01, 2:10, 0:45, 2:36, 1:25 min) before ejecting debris, whereas a beetle tunnelling into the epicarp of a hazelnut (*Corylus avellana*) gnawed for a total of 7:30 and 7:19 minutes before ejecting debris. In no instance did a beetle complete a full 360° rotation during tunnelling. In the majority of cases the beetle carried out only one turn before switching directions (Table 6). A full circle was recorded only during a debris removal sequence (*Phoenix canariensis*) when the beetle cleaned out the NW sector for 58 seconds and then turned clockwise. The majority of the stops in each octant was less than 15 seconds, with the exception of NE where the beetle spent 2 min 17 sec clearing out debris and the W octant, where the beetle spent 38 sec. The beetle continued to complete the full circle and then back-tracked counter-clockwise cleaning the next two octants again before recommencing tunnelling.

Table 5. Average duration (in sec.) of directional turns during tunnelling actions.

Sample	Hardness	Counter-clockwise		Clockwise		<i>p</i>
		Mean ± SD	<i>n</i>	Mean ± SD	<i>n</i>	
<i>Corylus avellana</i>	hard	24.23±19.69	13	13.43±13.40	21	0.097
<i>Washingtonia robusta</i>	medium	31.14±32.47	22	14.40±11.84	5	0.054
Tagua button blank	very hard	3.75±2.63	04	9.58±16.96	19	0.171
<i>Phoenix canariensis</i>	soft	117.41±115.92	17	103.30±77.35	20	0.672

Table 6. Frequency of consecutive turns in the same direction. *Phoenix canariensis* sample.

	Consecutive turns						<i>n</i>
	1	2	3	4	5	8	
Clockwise	9	-	2	1	-	-	12
Counter-clockwise	8	2	1	-	-	1	12
Total	17	2	3	1	1	1	24

Discussion

Coccotrypes dactyliperda tend to penetrate *P. canariensis* seeds in a systematic fashion with little variation. This appears to be driven by the nature of the seed's surface. The data show an overwhelming preference for penetration at the dorsal side and in particular the dorsal groove (unpubl. data). This is likely to have a biomechanical reason. In order to penetrate, the date stone beetle needs to be able to push its mandibles into the epicarp of the seed. As this requires some force, the beetle needs to find sufficient traction. Biomechanically, the main thrust of the tunnelling beetle is generated by the hind legs. Interpreting the footage, it appears that the mid legs function as a pivot, while the fore legs enable lateral control. We are less well informed once the beetle has created a full tunnel cavity, as observations are much more difficult. It would appear that inside the tunnel the pair of mid legs acts as wall anchors.

The convex shape of the recto side of *P. canariensis* seeds does not provide any traction, whereas the dorsal groove side allows the beetle to stem against one or both sides while penetrating. There is a preference to penetrate the proximal end of the dorsal groove, which is more irregular (unpubl. data). In his experiments with date stone beetles penetrating buttons made from Tagua nuts, Herfs (1948, 1950) observed the lack of traction on the smooth surfaces and noted that the beetles tended to penetrate the buttons from the thread holes. The same was observed by the present author among beetles penetrating polished and hard (dried out) tagua (corozo) buttons (Spennemann, 2018a). Similarly, the majority of hazelnuts that were offered to *C. dactyliperda* showed successful penetration as well as incomplete penetration events primarily on the rough surface of the proximal end or on its very edge, tunnelling into the sides. Where traction opportunities existed, penetration holes tended to be round where traction for the mid and/or hind legs was insufficient, penetration holes were more diffuse (Spennemann, 2018a). Seed hardness influences the duration of gnawing/tunnelling events. It is tempting to speculate that the volume of frass generated determines the duration of gnawing events between removal events. All observed repositioning movements occurred in octants, suggesting that the feeding/gnawing arc of the beetle was about 45° which equates to 22.5° from the beetle's main axis. A likely explanation for this is that the lateral movement of the pronotum is constrained to that angle.

Implications and further research

The study has shown that the tunnelling of *Coccotrypes dactyliperda* into seeds does not occur at random but follows specific patterns which seem to be governed by biomechanical constraints, in particular the ability of the beetle to gain traction. Once that is achieved, the beetle will carry out its penetration with frequent repositioning in octants. Based on the observations reported here future work may want to consider a multifactorial experiment to examine the nature of penetration and beetle behaviour using near identical seeds (such as *Phoenix canariensis*) but of different hardness (which could be simulated by artificially drying seeds for different durations). That experiment could also assess the overall speed of tunnelling. Finally, it would be interest to observe the penetration behaviour of *C. dactyliperda* on fresh (green) palm drupes. Whereas the albumen of the seeds is of a homogenous consistence, the epicarp of the drupes contains much fibrous matter which may influence tunnelling behaviour and speed.

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Conflict of Interests

The author declares that there is no conflict of interest regarding the publication of this paper.

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بررسی مشاهده‌ای نفوذ سوسک سنگی خرما (*Coccotrypes dactyliperda*) (Coleoptera, Curculionidae, Scolytinae) به بذر

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چکیده: سوسک سنگی خرما (*Coccotrypes dactyliperda* Fabricius, 1801) به بذور نخل تونل می‌زند تا گالری‌های نوزادان را ایجاد کند. لاروهای این حشره از آلبومین دانه تغذیه می‌کنند. براساس مشاهدات رفتاری، این مقاله پارامترهای بیومکانیکی لازم برای مراحل اولیه ایجاد تونل‌های لاروی و استقرار فضای پرورش نوزادان را توصیف می‌کند.

واژگان کلیدی: اسپرماتوفازی، رفتار تغذیه‌ای، تحرک، الگوی فعالیت