



Original article (Orijinal araştırma)

Resilience of breeding *Coccotrypes dactyliperda* Fabricius, 1801 (Coleoptera: Curculionidae: Scolytinae) to ingestion by vertebrates¹

Omurgalılar tarafından yutulan *Coccotrypes dactyliperda* Fabricius, 1801 (Coleoptera: Curculionidae: Scolytinae)'yı yetiştirmenin esnekliği

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Abstract

Volant and terrestrial predators consume a wide range of palm drupes, some of which may be infested by spermatophagus beetles. Field observations suggest that the larvae of some beetle species survive the passage through the gastrointestinal tract. To assess the resilience of the date stone beetle, *Coccotrypes dactyliperda* Fabricius, 1801 (Coleoptera: Curculionidae: Scolytinae) to ingestion by vertebrates, specimens reared from infested *Phoenix canariensis* (Chabaud, 1882) (Arecales: Areaceae) seeds were exposed *in vitro* to simulated gastric and intestinal fluids in a laboratory setting at Charles Sturt University (Albury, Australia) in 2018. The observed mortality among beetles protected in their galleries inside the seeds was low (11-24%). The continued breeding success was affected by numerous beetles abandoning the seeds after immersion. Total mortality occurred among unprotected beetles exposed for 12 h or longer. This study demonstrates that as mortality of adult beetles inside ingested seeds is very low, vertebrate vectors may aid in the medium- to long-distance dispersal of the species.

Keywords: Biogeography, digestion-resistant insects, endochory, insect pests, physiology

Öz

Kanatlı ve karada yaşayan predatörler, bazıları spermatofag böcekler ile bulaşık olabilen çok sayıda palmye meyvesini tüketmektedirler. Arazi gözlemleri, bazı böcek türlerinin larvalarının mide-bağırsak kanalından geçişte hayatta kaldıklarını göstermektedir. Bu makale, Hurma böceği, *Coccotrypes dactyliperda* Fabricius, 1801 (Coleoptera: Curculionidae: Scolytinae)'nın omurgalılar tarafından yutulmaya karşı direncini değerlendirmek amacıyla, enfekte olmuş *Phoenix canariensis* (Chabaud, 1882) (Arecales: Areaceae) tohumlarından yetiştirilen böcek örnekleri 2018 yılında Charles Sturt Üniversitesi (Albury, Avustralya)'ndeki bir laboratuvar ortamında *in vitro* da simüle edilmiş mide ve bağırsak sıvılarına maruz bırakılmıştır. Galerilerinde tohumların içinde korunan böcekler arasında gözlenen ölüm oranı düşük (%11-24) saptanmıştır. Sürekli yetiştirme başarısı, daldırmadan sonra tohumları terk eden çok sayıda böcekten dolayı etkilenmiştir. Toplam ölüm oranı, 12 saat veya daha uzun süre maruz kalan korunmasız böcekler arasında meydana gelmiştir. Bu çalışma, yutulan tohumlar içindeki ergin böceklerin ölüm oranı çok düşük olduğundan, omurgalı vektörleri sayesinde bu türlerin orta ila uzun mesafe dağılımına yardımcı olabileceğini göstermektedir.

Anahtar sözcükler: Biyocoğrafya, sindirime dirençli böcekler, endokori, zararlı böcekler, fizyoloji

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Introduction

The dispersal success of palms is enhanced by volant and terrestrial vectors which not only effect medium- to long-range transport of the seed away from the host tree (Zona & Henderson, 1989; Spennemann, 2018e), but also causes scarification of the seed coat during the passage through the gastrointestinal system which increases the likelihood of germination (Traveset, 1998; Rodriguez-Perez et al., 2005; Silverstein, 2005). The dispersal success of some palms, such as *Phoenix* sp., is affected by the presence and extent of infestation with date stone beetles, *Coccotrypes dactyliperda* Fabricius, 1801 (Coleoptera: Curculionidae: Scolytinae). Experiences during a seed germination experiment showed that *Phoenix canariensis* (Chabaud, 1882) (Arecales: Areaceae) seeds infested by these scolytids germinated (as evidenced by an emergent radicle), but that much of the albumen of the pericarp was consumed, thus dramatically reducing the viability of the developing hypocotyl to develop into a viable seedling (Spennemann et al., 2018).

Coccotrypes dactyliperda, is a spermatophagus beetle which is closely associated with the date palm, *Phoenix dactylifera* L., 1783 (Arecales: Areaceae) complex and can be considered endemic to the Middle East and North Africa. Due to the trade in dates as fruit for consumption, and during the nineteenth century also due to the distribution of palm seeds for horticultural endeavors and as vegetable ivory for button manufacture, *C. dactyliperda* has become a true cosmopolitan species that can be found in most subtropical and temperate zones (Spennemann, 2018b).

As with other crypto-parasites, the entire life cycle of *C. dactyliperda* occurs inside the seed. Mated females start to lay eggs 3 to 5 d after inhabiting a new seed. Unmated *C. dactyliperda* females are able to lay eggs that produce male offspring and then proceed to mate with these to produce offspring of mixed sex. Depending on the size of the seed, multiple broods and even generations of beetles can hatch and reproduce inside a seed before emerging. A single date seed can concurrently house large numbers of eggs, larvae, pupae and imagines, with in excess of 80 individuals (females, males, pupae, larvae and ova). On record is the development period of a full life cycle from egg to adult for females which is temperature- and humidity-dependent, and has been reported as ranging from 22 d (at 28°C) to 49 d (at 20°C). During the winter period imagines of female *C. dactyliperda* enter a hibernation or dormancy period inside the seed in which they hatched. After emergence from hibernation and subsequent oviposition, the first generation of female beetles to leave the brood chamber emerge during late-June to early-July (in the northern hemisphere) (Spennemann, 2019a).

Coccotrypes dactyliperda tend to either colonize within fallen seeds, or bore into fresh drupes on the infructescence causing their abscission. A study in Israel found that *C. dactyliperda* were responsible for about 20% of the annual seed bank found underneath palms 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 hibernation and the first generation in March, 95% of the seeds that had remained on the ground showed evidence of infestation (Bar-Shalom & Mendel, 2001).

Setting aside the random event that an infested drupe might be consumed by a bird during the short period prior to abscission, any dispersal of *Coccotrypes*-infested drupes will be due to birds (Spennemann, 2018d, 2019b) as well as terrestrial vertebrates, primarily canids and ursids (Spennemann, 2018e) feeding on fallen drupes.

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/gizzard (e.g., currawong; Spennemann, 2018d); or to partial digestion and subsequent defecation (e.g., canids). The survival of a *Coccotrypes* female and its brood will depend on the duration of exposure to gastrointestinal liquids (e.g., saliva, gastric acid and intestinal fluids), during gastrointestinal transit as well as the nature of ingestion and duration of mastication (if any).

The broader literature shows that while insect-infested fruit were rejected by birds (Manzur & Courtney, 1984) as well as primates (Benítez-Malvido et al., 2016), infestations of the seed, without significantly spoiling the pericarp (flesh) had a lesser adverse effect. Hernández (2011) reviewed instances where seeds infested by insects had passed partially (regurgitated) or fully (defecated) through the digestive system of birds (Nalepa & Piper, 1994; Guix & Ruiz, 1995, 1997; Hernández & Falcó, 2008), ungulates such as tapirs (Olmos et al., 1999; Giombini et al., 2009), marsupials (Rouco & Norbury, 2013), as well as primates (Bravo & Zunino, 1998; Bravo, 2008). Seed-inhabiting adult beetles in particular, had a high survival chance. However, in other examples, such as bruchid beetles, the ingestion and immersion in gastric fluids kills off large proportions of larvae inside the seeds (Lamprey et al., 1974; Coe & Coe, 1987; Or & Ward, 2003).

The extant literature is silent on the extent that mastication and ingestion of affected palm drupes might kill the beetles, pupae or larvae in the seed itself. The latter, in particular, have a permeable skin and therefore are susceptible to chemicals even in low concentrations, compared with the chitinous exoskeleton of adult beetles. In favor of survival are the comparatively short gastrointestinal transit times (see below), and the small diameter of the access hole (≤ 1 mm) which can easily be clogged by masticated matter. Moreover, female *C. dactyliperda* exhibit the behavior to block the entrance/exit of the brood chamber with their body to prevent larvae from falling out and stray matter to ingress (Spennemann, 2019a). As the bore hole is only marginally bigger than the diameter of the female beetle itself, that blocking may be very effective, as long as the beetle is resistant to the fluids it is exposed to.

While no experimental data exist that shed light on the ability of *C. dactyliperda* to survive ingestion, one anecdotal example, dating to the first half of the nineteenth century, has been documented in the literature. Hippolyte Lucas reports from Algeria in 1846 that the ingestion of infested *Chamerops humilis* L. seeds by Golden Jackals, *Canis aureus* L., 1758, (Carnivora: Canidae), which in North Africa are widely noted as feeding on fallen dates of *P. dactylifera* and other palms (Spennemann, 2018e), was reputedly not detrimental to the survival of *C. dactyliperda* beetles and their larvae (Lucas in Anonymous, 1846; Lucas, 1849).

Coccotrypes dactyliperda have shown a great resilience to adverse external environmental conditions. In previous work, the author exposed cohorts of *C. dactyliperda* to insecticides (Spennemann et al., 2018) as well as subzero temperatures (Spennemann, 2019c). While the galleries could not provide sufficient protection to prolonged exposure to freezing (80% mortality after 7 h at -8°C), the beetles were surprisingly resilient to some but not all insecticides. While mortality was only 14.3% following a 20 min immersion in 10% bleach, the mortality was 33.3% among seeds that had been immersed in the synthetic pyrethroid Cyhella®. An exposure to the organophosphate Fenitrothion®, however, caused 87.5% mortality (Spennemann et al., 2018).

This paper will report on the findings of experiments designed to simulate the ingestion of *C. dactyliperda* by vertebrates and the exposure of breeding females to gastric and intestinal fluids.

Materials and Methods

To simulate ingestion by predators, beetles in their seeds were exposed to an immersion in simulated gastric and intestinal fluids (for composition see below). The experiment did not simulate the mechanical mixing and potential grinding action that occurs in the crop or stomach, nor the movement the seeds would experience in the intestinal tract. Two sets of samples were prepared, one which was immersed in 50 ml clear fluids and one that was immersed in a simulated masticated pulp comprised of 50 g fruit pulp mixed with 50 ml simulated gastric fluid (SGF) or simulated intestinal fluid (SIF). Samples using plain tap water served as a control.

The experiment was conducted in October 2018 in the PC2 laboratory of the Peter Till Laboratories, Faculty of Science, Charles Sturt University (Albury, Australia).

Source of the beetles

The beetles used here were drawn from a population bred for a multifactorial experiment, assessing food choices and emergence times (Spennemann, 2018a). The original beetle population originated from *P. canariensis* seeds collected at Alma Park, NSW, Australia (Spennemann et al., 2018).

Preparing seed used in the experiment

For the exposure experiments, beetles were either used unprotected (i.e., by themselves in a vial) or protected in their galleries (to simulate real conditions). In order to avoid previous experiences with collective exposures, where single seeds were penetrated by multiple beetles (Spennemann, 2018a), single beetles were placed with a single seed each into 7.5 ml plastic vials. These beetles were allowed to tunnel for 6 to 9 d. As mated females start to lay eggs between 1 and 3 d after inhabiting a new seed (Herfs, 1950; Zchori-Fein et al., 2006), the eight-day period was deemed sufficient for each beetle to establish a breeding gallery. As some beetles refused to take to a seed and had to be replaced after 3 d, the seeds were then extracted and, as cohorts of 10, were subjected to various treatments (see below). Common to all seeds were single penetration holes of 1 mm diameter (Figure 1a).

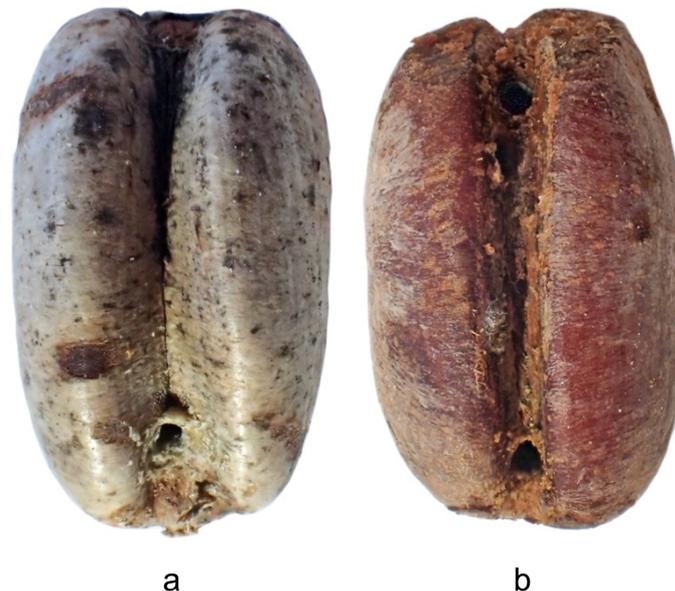


Figure 1. Examples of penetrated seeds used for the experiment: a) single penetration hole (at bottom of image); b) single penetration hole (bottom) and two exit holes (top of image).

The actual depth of the penetration was not ascertained at the start of the immersion. Some had commenced tunneling but had abandoned these tunnels. This was not noticed at the commencement of the experiment and was only recognized when the seeds were cut open at the end of the experiment. This accounts for the smaller sample numbers in Table 3.

The beetle-infested seeds used for the long-term immersion in simulated intestinal fluid mixed with pulp (12 and 24 h) were drawn from a breeding population where many of the beetles were already in a more advanced stage of development and the seeds already exhibited multiple exit holes (Figure 1b). These seeds had, therefore, a greater probability of moisture intrusion into the gallery.

Simulated gastric and intestinal fluids

Simulated gastric and intestinal fluids are commonly used to study questions such as the digestibility and performance of foods (Fu et al., 2002; Stappaerts et al., 2014), the solubility and dissolution behavior of drugs (Khadra et al., 2015; Wang et al., 2015) and drug delivery methods (Chen et al., 2018). The composition of the simulated gastric and intestinal fluids used in this experiment follows the formulation described by Wang et al. (2015):

Simulated gastric fluid - 0.8 g of sodium chloride was dissolved in 100 ml of reverse osmosis (RO) water. 2.8 ml of 10M HCl was then added to the NaCl solution to adjust the pH 1.2. To this, 1.28 g of Pepsin was added and gently stirred. The volume was then made up to 400 ml with RO water. The solution had a final pH of 1.55.

Simulated intestinal fluid - 2.72 g of monobasic potassium phosphate was dissolved in 100 ml of RO water, then 44.7 ml of 0.2 N NaOH was added to adjust the pH to 6.8. To this, 4 g of Pancreatin was added and gently stirred. The volume was then made up to 400 ml with RO water. The solution had a final pH of 6.84.

To create simulated masticated fruit pulp, the flesh was removed, from 300 fresh *P. canariensis* drupes (peeled *in toto* or flesh cut off in strips), which yielded 319 g of flesh. The sample of flesh pieces was mixed thoroughly. 25% were retained as peeled and the remaining 75% were chopped in a domestic kitchen blender. 50% of this mass was removed, with the remainder pureed. All three fractions (Figure 2) were then combined.



Figure 2. Fractions of palm flesh pulp. From left: as peeled; chopped; pureed.

The minimum time of exposure of the beetles to the clean seeds was 7 d and the maximum time was 10 d. To ensure that these time differences did not affect the outcomes in a systematic fashion, the 80 vials were randomly allocated to one of eight cohorts of 10 [numbers 1-80 allocated at random, then groups in sets of 10 (A-H)]. These eight cohorts were then randomly allocated to the experiments.

At the time of exposure to the experimental fluids or pulp mixtures, a cohort of ten live beetles was directly added to the container to simulate the incidental ingestion of crawling specimens. Once exposed to the sample solution, the samples were vigorously shaken for 10 s at 5-min intervals, but were otherwise left to sit on the lab bench.

Duration

Assessed was the survival of *C. dactyliperda* at intervals from 0.3 to 24 h. The duration of exposure to the fluids was informed by data on gastrointestinal transit times in the primary vectors. Among birds there appears to be not only a correlation between body size (and thus gape size) and the size of fruit consumed, but also between body size and retention time in the crop until regurgitation, with larger birds retaining larger seeds for longer periods (Levey, 1987). Among Pied Currawongs, *Strepera graculina* (Shaw, 1790) (Passeriformes: Artamidae) for example, it takes between 5 to 15 min after ingestion to regurgitate the rough and indigestible matter (e.g., seeds, epicarp, fibrous parts of pericarps, bones and feathers) in the form of pellets (Bass, 1995). Among canids, gastrointestinal transit time appears to be related to body size. It is significant that not all stomach content is necessarily defecated at the same time, with some content delayed up to 30 h. Observed transit times range from 3 h [Red Foxes, *Vulpes vulpes* L., 1758 (Carnivora: Canidae)] to 55 h [large domestic dogs, *Canis familiaris* L., 1758 (Carnivora: Canidae)] (Neseni et al., 1955; Szuman & Skrzydlewski, 1962; Weber, 2006; Boillat et al., 2010).

Exposure time for each liquid was set at 20 min, with the exception of a sequential exposure to both simulated gastric and intestinal fluid (20+20 min). To assess the effects of longer gastrointestinal transit times, isolated beetles (in cohorts of 10) were placed into 7.5-ml vials and exposed to SGF and SIF for up to 24 h.

Assessment and disposal of survivors

At the end the respective set time intervals the samples were drained on filter paper, and the seeds extracted. The residue was searched to assess the survival of the isolated beetles. Any specimens found alive were killed in 90% alcohol. The entire pulp residue was then placed into a freezer at -12°C for 5 d to kill any beetles that had not been located. A similar procedure was followed for the beetles emerging from the seeds (see below) and the final disposal of the infested seeds. At the termination of the experiment 27 d after immersion (34-37 d after commencement), all seeds that had not yielded two emergences were cut open and inspected. Given the life cycle of *C. dactyliperda* comprised of an egg incubation period (6-10 d), larval stage (12-15 d) and pupal stage (3-4 d) (Spennemann, 2019a), the presence of pupae was interpreted as evidence of successful breeding.

The extracted seeds were placed in numbered vials to observe the emergence success and timing. At the time of exposure, the brood chamber would have comprised of the adult female as well as eggs and some larvae (for life cycle times see Spennemann, 2019a). The emergence of more than one adult beetle was taken as evidence of successful continued breeding as the second individual must have developed from eggs (or larvae) present at the time of immersion, or from subsequent oviposition events.

Statistical analysis

Statistical analysis of the small sample was limited to exploratory analysis (Tukey, 1980), primarily using the statistical functions in MS Excel and the two-proportion z-test (Stangroom, 2019).

Results

The results of the simulated ingestion by drupe predators are set out in Table 1. Note that despite diligent searching, one beetle each could not be located in the pulp samples H₂O and SGF (indicated by the + sign). At least in the instance of the control sample (H₂O) it must be assumed that the missing beetle was alive. As anticipated, all isolated beetles survived the control experiment despite the vigorous shaking.

Intriguingly, the survival rate of the beetles exposed to SGF was likewise high, where exposure to liquid SIF resulted in 50% mortality. The presence of pulp buffered the effects of SIF, with nil mortality in the sample of SIF alone, and 30% mortality in the sequential SGF-SIF experiment. The higher mortality in the latter experiment may have been caused by the greater volume of liquid in that sample (50 g of pulp immersed in 50 ml of SGF and SIF each) as exposed to the stand-alone SIF experiment (50 g of pulp immersed in 50 ml of SIF).

Table 1. Resistance of *Coccotrypes dactyliperda* to ingestion (in % of seeds) using simulated gastric fluid (SGF) and simulated intestinal fluid (SIF) (Statistically significant ($p < 0.05$) difference from the control shown in bold italics)

Treatment		liquid				pulp							
		20 min		40 min		20 min		40 min		12 h		24 h	
		single	in seed	single	in seed	single	in seed	single	in seed	single	in seed	single	in seed
	H ₂ O	100	71.4	—	—	90+	62.5	—	—	—	—	—	—
	SGF	90	66.7	—	—	90+	85.7	—	—	—	—	—	—
	SIF	50	62.5	—	—	100	44.4	—	—	0	88.9	0	87.5
	SGF/SIF	—	—	50	66.7	—	—	70	44.4	—	—	—	—

A subsequent experiment examined the effects of longer exposure of single beetles to both simulated fluids. Notably, the mortality among the beetles exposed to SIF was much less in this experiment, at least in the early stages (Table 2). Although it is possible that, despite repeated vigorous mixing, the increased surface tension in the smaller vial contributed to the beetles remaining partially afloat, the beetles were fully exposed to the fluids. All beetles immersed in tap water were alive after a 24 -h period. In a different experiment with an identical methodology, *C. dactyliperda*, were alive even after a 48-h immersion in tap water (Spennemann et al., 2018). Beetles immersed in SGF survived to a large degree until more than 6 h had passed and then mortality increased (Table 2; Figure 3). The observed differences between the control and SGF became statistically significant (two proportion z-test; $p < 0.05$) only after 12 h of immersion (24 h, $z=2.58$, $p=0.01$). Immersion in SIF had a much greater impact, mortality remained low until 1 h after immersion, when it dropped dramatically. At 1.5 h only 30% were still alive, which was a statistically significant decrease ($z=3.28$, $p=0.001$). Mortality remained at the 30% level until after 9 h of immersion, when it rose to 100%.

Table 2. Resistance of single *Coccotrypes dactyliperda* to ingestion (immersion in liquid) using simulated gastric fluid (SGF) and simulated intestinal fluid (SIF) (Statistically significant ($p < 0.05$) difference from the control shown in bold italics)

Treatment	Exposure time (h)										
	0.5	0.75	1	1.5	2	3	4	6	9	12	24
H ₂ O	10	10	10	10	10	10	10	10	9	10	10
SGF	10	9	10	8	8	8	8	9	6	7	5
SIF	10	10	8	3	2	3	3	3	3	0	0

The beetles that resided in the seeds when exposed to fluids exhibited a low mortality (Table 3). Only in the case of an immersion in SGF and SIF mixed with pulp did some beetles die (22.2%). That rate of mortality was not statistically significantly different from immersion in H₂O ($\chi^2=1.66$; $p=0.197$), or SIF ($\chi^2=2.12$; $p=0.145$) or SGF ($\chi^2=1.67$; $p=0.197$) alone. The continued breeding success, however, was affected by numerous beetles that abandoned the seeds after immersion. As this also occurred in the H₂O controls (Table 3), it was caused by environmental factors in the vials rather than the exposure per se. Indeed, the observed differences in the rate of abandonment (Table 3) are not statistically significant (Table 4).

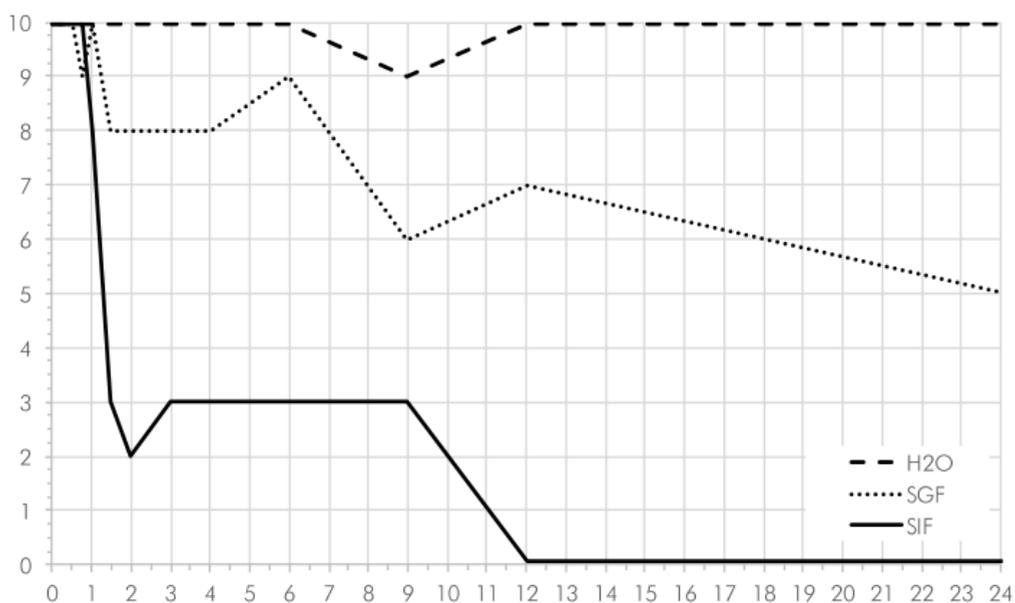


Figure 3. Resistance of single *Coccotrypes dactyliperda* to ingestion using simulated gastric fluid (SGF) and simulated intestinal fluid (SIF) over time (24 h).

Table 3. Resistance of *Coccotrypes dactyliperda* breeding in seeds to ingestion using simulated gastric fluid (SGF) and simulated intestinal fluid (SIF) (in % of seeds)

		Success	Abandoned	Mortality	n
H ₂ O	clear	71.4	28.6	0.0	7
	pulp	62.5	37.5	0.0	8
SGF	clear	66.7	33.3	0.0	6
	pulp	85.7	14.3	0.0	7
SGF/SIF	clear	66.7	33.3	0.0	9
	pulp	44.4	33.3	22.2	9
SIF	clear	62.5	37.5	0.0	8
	pulp	44.4	55.6	0.0	9
	pulp 12	88.9	11.1	0.0	9
	pulp 24	87.5	12.5	0.0	8

Table 4. Differences in percentages of abandoned seeds between the control and simulated gastric fluid (SGF) or simulated intestinal fluid (SIF)

	H ₂ O	SGF	SIF	SGF/SIF	
H ₂ O	—	$\chi^2=0.031$; $p=0.8604$	$\chi^2=0.124$; $p=0.7245$	$\chi^2=0.038$; $p=0.038$	clear fluid
SGF	$\chi^2=0.959$; $p=0.3275$	—	$\chi^2=0.027$; $p=0.8699$	$\chi^2=0.001$; $p=0.9805$	
SIF	$\chi^2=0.524$; $p=0.4691$	$\chi^2=2.686$; $p=0.1013$	—	$\chi^2=0.023$; $p=0.8807$	
SGF/SIF	$\chi^2=0.023$; $p=0.8807$	$\chi^2=0.750$; $p=0.3865$	$\chi^2=0.809$; $p=0.3683$	—	
pulp					

Discussion

The literature reports a number of instances where insects successfully hatched from ingested infested seed. The base assumption is that the seeds were infested when the drupe still had a substantial amount of pericarp adhering, which acted as an attractant to the fruit disperser. Some species, such as *Revena rubiginosa* (Boheman, 1836), (Coleoptera: Curculionidae) will perforate a developing drupe for oviposition in the seed, but will not inhabit the seed itself (Martín et al., 2009). Larvae emerged successfully from *R. rubiginosa*-infested *Syagrus romanzoffiana* (Cham.) Glassman (Arecales: Arecaceae) drupes regardless of whether the seeds were regurgitated (Guix & Ruiz, 1995) or defecated by birds (Guix & Ruiz, 1997) or defecated by ungulates (tapirs) (Olmos et al., 1999).

While *R. rubiginosa* in *S. romanzoffiana* seeds seem to survive the passage through a tapir's digestive tract (Olmos et al., 1999), *Pachymeris cardo* (Fåhræus, 1839) (Coleoptera: Chrysomelidae) (a bruchid beetle) in *Maximiliana maripa* (Aubl.) Drude (Arecales: Arecaceae) seed exhibited a high mortality in tapir guts (Fragoso, 1997). This is supported by other examples of bruchid beetles, where the ingestion and immersion in gastric fluids kills a large proportion of larvae inside seeds (Lamprey et al., 1974; Coe & Coe, 1987; Or & Ward, 2003). The high mortality among bruchids can be explained by the fact that oviposition, and subsequent early larval development, occurs on the surface of the drupe/seed rather than inside (Ernst et al., 1990) and that the damage to the epicarp is more extensive (due to numerous penetration holes by multiple larvae).

Coccotrypes dactyliperda, as described, will penetrate a drupe (or seed) and will complete its entire life cycle inside the seed. This results in a single penetration hole, limiting the ingress of gastric acids. Moreover, it can be speculated that adult beetles, with their chitinous exoskeleton, are more resilient to the impact of low-concentration acidity than larvae with their soft and moisture-dependent skin. Even if larvae were to die due to exposure, but if the adult beetle survives, the female may either lay fresh eggs or abandon the seed and recommence breeding elsewhere. The data presented here support this conceptual model. It could be shown that *C. dactyliperda* inside seeds will survive ingestion and subsequent regurgitation or defecation by vertebrates. Some will continue breeding, while others will abandon their seed to search for a new seed. The experiments also indicate that *C. dactyliperda* will survive exposure to gastric and intestinal fluids for a short time even if they are not protected by the seed. This suggests that while they may be killed prior to defecation by terrestrial mammals, they might survive the comparatively short period between ingestion and regurgitation among birds.

As these were *in vitro* rather than *in vivo* experiments, the experiments could neither take into account the mechanical action during mastication, nor that which takes place in the crop and gizzard of the birds or the stomach on terrestrial vertebrates. It is speculated that such action might crush or otherwise affect beetles crawling among the food mass and that the action may push some of the food mass into the tunnel. Among mammals, seed damage caused by mastication is usually low (Koike et al., 2008), unless the seeds have been hollowed out so far that they can be crushed easily (Or & Ward, 2003).

Conclusions

Based on the experiments, it is clear that *C. dactyliperda* breeding in *P. canariensis* seeds, and presumably seeds of other palm species, will survive ingestion and passage through the gastrointestinal tract and may be transported and dispersed by vertebrates with long gastrointestinal transit times, such as canids. Thus, vertebrate vectors may aid in the medium- to long-distance dispersal of the beetle. While the beetles may survive the gastrointestinal passage and may successfully reproduce after defecation, the ultimate success of the population will depend on whether the emerging beetles will be able to find suitable host seeds at the new locality.

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