INTERAÇÃO INDIRETA: A HERBIVORIA DE ÁCAROS AOS FRUTOS DE COQUEIRO INTERFERE NA HISTÓRIA DE VIDA DE *Atheloca bondari* (LEPIDOPTERA: PYRALIDAE)

por

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RESUMO

Interação intermediada por alterações fenotípicas de plantas é um evento frequente nos mais diversos ecossistemas e de grande importância para a formação das comunidades de herbívoros. O ataque de um herbívoro pode reduzir a quantidade de alimento disponível, ou induzir alterações químicas, estruturais, morfológicas e fenológicas na sua hospedeira. Essas modificações na planta potencialmente interferem na distribuição, desempenho e comportamento de outras espécies que compartilham a hospedeira, mesmo que separados espaço-temporalmente. A alteração na região externa do fruto de coqueiro (*Cocos nucifera*) potencialmente modifica o padrão de ocorrência de herbívoros na planta. Em coqueiro, *Aceria guerreronis* (Acari: Eriophyidae), *Steneotarsonemus concavuscutum* (Acari: Tarsonemidae) e *Atheloca bondari* (Lepidoptera: Pyralidae) desenvolvem-se sob o perianto dos frutos de coqueiro. Um estudo taxonômico foi realizado para confirmar que *At. bondari* é a espécie de ocorrência no Brasil. Os ácaros causam necroses no epicarpo dos frutos, e as necroses de *Ac. guerreronis* frequentemente promovem rachaduras, enquanto as necroses e *S. concavuscutum* não. As larvas de *At. bondari* utilizam as rachaduras da necrose causada por *Ac. guerreronis* para infestar os frutos. A distribuição de *At. bondari* na palmeira é influenciada pela presença ou ausência de *Ac. guerreronis* nos frutos, além disso, a infestação de *At. bondari* está correlacionada com o maior abortamento de frutos. A infestação por ácaros aos frutos afetou distintamente o desempenho e preferência de *At. bondari*, onde os frutos infestados por *Ac. guerreronis* receberam um maior número de ovos e melhoraram o desempenho de *At. bondari*. A infestação de *S. concavuscutum* aos frutos modificou a preferência de oviposição das fêmeas, mas não interferiu no desempenho das larvas de *At. bondari*. A importância de *At. bondari* como praga do coqueiro está diretamente relacionada com a presença de *Ac. guerreronis*.

PALAVRAS-CHAVE: *Cocos nucifera*, interação mediada por característica da planta, ácaro do coqueiro, facilitação.

INDIRECT INTERACTION: MITES HERBIVORY TO COCONUT AFFECT THE LIFE HISTORY OF *Atheloca bondari* (LEPIDOPTERA: PYRALIDAE)

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ABSTRACT

Interaction mediated by phenotypic changes in plants is a frequent event in the most diverse ecosystems and import for the formation of herbivore communities. Attack by herbivores can reduce the amount of food available, or induce chemical, structural, morphological and phenological changes in its host. These changes in the plant potentially interfere with the distribution, performance and behavior of other species that share the host plant, even if spatial-temporally separated. The arrival of a first herbivore may decrease the amount of food available for a subsequent herbivore, or induce chemical, structural, morphological, phenological changes in the host plants. The change in the external region of the coconut fruit (*Cocos nucifera*) potentially changes the pattern of herbivore occurrence in the plant. In coconut palm, *Aceria guerreronis* (Acari: Eriophyidae), *Steneotarsonemus concavuscutum* (Acari: Tarsonemidae) and *Atheloca bondari* (Lepidoptera: Pyralidae) develope under the perianth of coconut fruits. A taxonomic study was performed to confirm that *At. bondari* is the species that occurs in Brazil. The mites cause necrosis in the epicarp of coconut, where *Ac. guerreronis* necroses often cause cracks, while necroses of *S. concavuscutum* do not. *Atheloca bondari* larvae use the cracks of necrosis caused by *Ac. guerreronis* to infest the coconuts. The distribution of *At. bondari* in the coconut field is influenced by the presence or absence of *Ac. guerreronis*, moreover, we show that

At. bondari infestation is correlated with the largest fallen fruits. Mites-infested fruits distinctly affected the performance and preference of *At. bondari*, where *Ac. guerreronis*-infested fruits received a larger number of eggs and improved the performance of *At. bondari*. *Steneotarsonemus concavuscutum*-infested fruits modified the oviposition preference of females but did not affect the performance of *At. bondari* larvae. The importance of *At. bondari* as a coconut palm pest is directly related to the presence of mites.

KEY WORDS: *Cocos nucifera*, plant-trait mediated interaction, coconut mite, facilitation interaction, mariposa do coqueiro

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> “The secret of wisdom, power and knowledge
>
> is **humility**”
>
> (Ernest Hemingway)

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SUMÁRIO

CAPÍTULO 1

INTRODUÇÃO

Observar os padrões de distribuição de espécies na natureza não é uma prática recente. Na Grécia antiga, por exemplo, o filósofo Aristóteles e seu aprendiz Teofrasto já encontravam padrões de ocorrência entre espécies de animais e plantas (Hughes 1985). Embora fosse possível encontrar relações de ocorrência, os mecanismos responsáveis pela estruturação e estabilidade das associações dos organismos permaneciam desconhecidos, sendo esse um tema central nos estudos ecológicos atuais (Ruiter *et al*. 1995, Williams & Martinez 2000, Ives & Carpenter 2007, Benkman 2013, Chamberlain *et al*. 2014, Morlon *et al*. 2014, Tang *et al*. 2014, Allesina *et al*. 2015). Conhecer os padrões de estruturação de comunidades é importante, e pode ser utilizado para fazer previsões de como o aquecimento global, atividades antrópicas, desastres naturais, e outros impactos de curto ou longo prazo, interferem no equilíbrio dos ecossistemas naturais (Ezard *et al*. 2010, Valiente & Banuet *et al*. 2015, Wright *et al*. 2015, Thompson *et al*. 2017, Arnoldi *et al*. 2018).

Na natureza, redes comunitárias multidimensionais são formadas através de interações entre populações que compartilham o mesmo ambiente. May (1972) demonstrou que a complexidade ecológica (definido como o número de interações de espécies e da frequência das suas interações) restringe a estabilidade das redes de interações. Esse importante resultado sugere que, apesar da complexidade dos ecossistemas, as redes reais devem ter mecanismos não aleatórios que permitem a persistência estável dos ambientes naturais (Bascompte 2010). A arquitetura das redes e os tipos de interações (por exemplo mutualística, antagonística, etc) são mecanismos que desempenham um impacto notável nos perfis de estabilidade da dinâmica de comunidades dentro dos ecossistemas (Thébault & Fontaine 2010, Allesina & Tang 2012, Mougi & Kondoh 2012).

As espécies podem se conectar através de redes tróficas (teias alimentares) e não tróficas (facilitação, mutualismo, competição, etc) (Kéfi *et al*. 2012, Guerrero-Ramírez & Eisenhauer 2017). Ambas as interações podem provocar, direta ou indiretamente, efeitos positivos ou negativos nas populações integrantes de comunidade. Todavia, interações diretas de modularidade negativa como predação (interações predador-presa) e competição (por exploração ou interferência) dominaram historicamente os estudos sobre estruturação e estabilidade das comunidades (Nicholson 1933, Gause 1934, Paine 1980, Connel 1983, Tilman 1994, Ruiter *et al*. 1995, Tang *et al*. 2014, Allesina *et al*. 2015). Em decorrência disso, entre os anos de 1960 e 1970, interações competitivas foram consideradas como o centro da força de organização das assembleias de insetos fitófagos (Connell 1983, Schoener 1983, Jermy 1985, Denno *et al*. 1995). Durante essas décadas os estudos foram dominados por investigações de campo relacionando a partição de recursos como evidência para a redução da competição e coexistência de espécies (Denno *et al*. 1995). Desta forma, o padrão de distribuição irregular, tanto em relação a fenologia do hospedeiro (deslocamento temporal) quanto na utilização de diferentes tecidos vegetais (deslocamento espacial), de insetos herbívoros que compartilham a planta hospedeira, era considerado como uma estratégia para permitir a coexistência estável (Schoener 1974, Connell 1980).

A observação da coexistência entre herbívoros dentro da mesma planta e associações de densidade positiva entre espécies competidoras (Ross 1957, Rathcke 1976, Lawton 1982, Strong 1982) fez com que alguns entomologos questionassem a relevância da competição como uma das principais forças na organização e estruturação de comunidade de insetos herbívoros (Strong *et al*. 1984, Jermy 1985). A partir da metade da década de 80, estudos empiricos surgiram dando robusto suporte para a competição indireta envolvendo insetos herbívoros (Harrison & Karban 1986, Karban 1989). Karban & Denno (1997) publicaram um livro exemplificando situações, nas quais os herbívoros interagem indiretamente através de modificações na planta hospedeira. Efeitos indiretos ocorrem quando a interação entre duas espécies é intermediada por modificações tanto da densidade quanto de características de uma terceira espécie integrante da comunidade (Abrams *et al*. 1996). Efeitos indiretos mediados por densidade resultam em uma resposta numérica e predominam nas interações predador-herbívoro, enquanto os mediados por características influenciam comportamento, morfologia, fisiologia e histórias de vida das espécies induzidas, e são de importância primária nas interações planta-herbívoro (Ohgushi 2005, 2007). Desta forma, incorporar as conecções indiretas dentro das redes de interações tróficas oferece uma melhor perspectiva sobre como as comunidades se mantém estáveis nos ecossistemas (Kaplan & Denno 2007, Ohgushi *et al*. 2007).

As modificações de caractéristicas das plantas em decorrência do ataque de herbívoros é um evento onipresente em comunidades de plantas (Karban & Baldwin 1997, Werner & Peacor 2003, Ohgushi 2005, Ohgushi 2008), sendo reconhecido como um importante determinante da composição da comunidade de herbívoros (Rodriguez-Saona *et al*. 2005, Kaplan & Denno 2007, Anderson *et al*. 2009, Stam *et al*. 2014). A herbivoria pode induzir a produção de metabólitos químicos de defesa em plantas (Haukioja & Neuvonen 1987, Kessler & Baldwin 2002, Kant *et al*. 2015) que funcionam como um inibidor de crescimento e desenvolvimento de herbívoros, e consequentemente reduz a pressão dos herbívoros sobre as plantas (Agrawal 1998). O ataque de herbívoros também pode induzir modificações morfológicas nas plantas, como aumento da produção de espinhos (Gómez & Zamora 2002) e tricomas (Agrawal 1999, Dalin & Bjorkman 2003). A qualidade nutricional da planta hospedeira pode também ser alterada em decorrência do ataque de herbívoros (Denno *et al*. 2000, Fukui *et al*. 2002). Além disso, herbívoros podem modificar fisicamente a planta através da formação de galhas, minas, abrigos foliares e perfurações em troncos, de maneira que essas estruturas possam ser utilizadas como abrigo por outros herbívoros (Lill & Marquis 2003, Nakamura *et al*. 2003, Kagata & Ohgushi 2004, Cornelissen *et al*. 2016). Nesse contexto, efeitos indiretos mediados por modificações de características das plantas induzidas por herbivoria tem potencial de ligar múltiplas interações de artrópodes em comunidades (Ohgushi 2008, Anderson *et al*. 2009).

As plantas respondem ao ataque de herbívoros de maneira altamente específica (Kessler & Baldwin 2002, Kessler & Halitschke 2007), desta forma, a diferenciação na ordem de chegada dos herbívoros pode interferir na estruturação das comunidades de insetos que compartilham plantas hospedeiras (Poelman *et al*. 2008, Stam *et al*. 2014, Stam *et al*. 2018). Além disso, plantas quando atacadas por mais de um herbívoro respondem de maneira distinta em comparação ao ataque de um único herbívoro, assim, a presença de um ou múltiplos herbívoros na planta hospedeira pode induzir diferentes características e desta forma diferir quanto a resposta no desempenho ou preferência de um herbívoro subsequente (Poelman *et al*. 2008, Mathur *et al*. 2013, Kroes *et al*. 2016). Apesar dos efeitos de modularidade negativa receberem maior atenção, herbívoros podem afetar positivamente espécies concorrentes através de alteração de características das plantas, como a melhoria nutricional (por exemplo aumentando a concentração de nitrogênio nas folhas) e/ou aumento da biomassa das plantas (por exemplo induzindo o crescimento de ramos laterais) (Strauss 1991, Pilson 1992, Fukui 2001), interferência na indução de defesa química (por exemplo *crosstalk*) (Glas *et al*. 2014, Stam *et al*. 2014) ou criando habitat dentro da planta (Martinsen *et al*. 2000, Lill & Marquis 2003, Harvey *et al*. 2015).

Espécies que modificam fisicamente o ambiente e, por consequência, controlam direta ou indiretamente a disponibilidade de recurso para outro organismo são reconhecidas como *ecosystem engineers* (Jones *et al*. 1994, 1997). A importância de um construtor (*ecosystem* *engineers*) para um artrópode em particular (inquilino) vai depender do valor do habitat modificado em contraste com o habitat que não foi modificado. Esse valor deve estar em função das diferenças entre os dois tipos de habitat e deve ser influenciado pela intensidade de estresse abiótico, qualidade relativa do alimento, interação de competição ou mutualismo, e resposta aos inimigos naturais (Marquis & Lill 2007). Desta forma, a força da interação entre o construtor e inquilino pode levar a uma dinâmica de coevolução contínua (Ehrlich & Raven 1964, Abrams 2000, Case & Taper 2000), dependendo do nível de pressão seletiva imposta pelo habitat modificado. Devido a possibilidade de a modificação física causada por um herbívoro coincidir com alteração da qualidade nutricional do alimento, o construtor pode interferir tanto na disponibilidade do recurso, como também no desempenho dos inquilinos (Larsson *et al*. 1997, Fukui 2001, Fukui *et al*. 2002). Apesar de muito conhecido em ambientes naturais, as interações indiretas mediadas por características de plantas induzidas por herbivoria são pouco estudadas em ambientes agrícolas (Kaplan & Denno 2007, Eubanks & Finke 2014), e isso ocorre possivelmente devido a utilização de táticas de controle, que interferem nas interações antes que elas aconteçam. No presente estudo foi utilizado um modelo envolvendo três herbívoros considerados pragas da cultura do coqueiro (*Cocos nucifera* L.), *Aceria guerreronis* (Acari: Eriophyidae) (Keifer), *Steneotarsonemus concavuscutum* (Acari: Tarsonemidae) Lofego & Gondim Jr. e *Atheloca bondari* Heinrich (Lepidoptera: Pyralidae). Foi avaliado como os danos aos frutos do coqueiro causados pelos ácaros medeiam a disponibilidade de abrigo interferindo na distribuição, preferência e desempenho de *At. bondari*.

Através da revisão de literatura observou-se que *At. subrufella* foi a espécie inicialmente relatada no Brasil (Bondar 1940), até então a única espécie do gênero. Heinrich (1956) revisou os espécimes de ocorrência no país e encontrou diferenças, resolvendo então por descrever uma nova espécie (*At. bondari*). Contudo, essa informação parece ser totalmente ignorada, tanto que os estudos atuais com essa mariposa consideram a informação de G. Bondar e não a de C. Heinrich (Bento *et al*. 2006, Sarro *et al*. 2007, Santana *et al*. 2009, 2010a, 2010b, Nascimento *et al*. 2016), o que tem causado confusão quanto a verdadeira identidade taxonômica. Por isso, primeiramente foi realizado um estudo taxonômico da espécie para resolver essa questão que se encontra em aberto.

O fruto do coqueiro é uma drupa formado por um epicarpo que pode ser de várias cores (verde, vermelho, amarelo, etc), um mesocarpo espesso e fibroso e internamente um endocarpo bem duro, no interior do qual existe o albúmen líquido (água de coco) e o albúmen sólido (copra ou carne do coco) (Smit 1970). Na extremidade apical do fruto um grupo de sépalas (conhecido comumente por perianto) cobre a região meristemática (Howard & Rodriguez 1991, Moore *et al*. 2001).

A extremidade distal do perianto funciona como uma defesa física do fruto pois limita a entrada de organismos na região meristemática dos frutos (Howard & Rodriguez 1991, Aratchige *et al*. 2007). Todavia, espécies fitófagas diminutas com habilidade de ultrapassar esta barreira física conseguem acessar um local que poderá fornecer recursos ao seu desenvolvimento, ao mesmo tempo em que proporcionará proteção a inimigos naturais. A região meristemática é um local de difícil acesso para a maioria dos herbívoros, pois para alcançá-la é preciso ultrapassar o espaço entre o epicarpo do fruto e a extremidade distal do perianto. Este espaço, dependendo da variedade, mede entre 41 e 99 µm (Aratchige *et al*. 2007, Lima *et al*. 2012). As fêmeas adultas de *Ac. guerreronis* medem entre 36-52 µm de altura (Keifer 1965) o que permite que esse ácaro acesse e inicie sua colônia na região meristemática dos frutos. *Steneotarsonemus concavuscutum* é outro ácaro frequentemente encontrado na região meristemática dos frutos de coqueiro, ocupando o mesmo habitat que *Ac. guerreronis* (Lawson-Balagbo *et al.* 2008).

Os frutos de coqueiro infestados por *Ac. guerreronis* e S. *concavuscutum* desenvolvem diferentes níveis de necrose no epicarpo. A necrose causada por *Ac. guerreronis* facilita a infestação da mariposa *At. bondari* na região meristemática dos frutos (Santana *et al*. 2009). *Atheloca bondari* é uma praga secundária, geralmente considerada sem importância, mas que em algumas situações pode afetar economicamente a produção de coco. De acordo com Ferreira *et al.* (2002) a importância de *At. bondari* pode variar de acordo com a região, condições climáticas e, principalmente, com as táticas de manejo adotadas na condução da cultura. De modo geral, áreas de grande produção, onde é implementada táticas para controle das pragas consideradas primárias (por exemplo *Ac. guerreronis*), *At. bondari* não representa problema econômico. Isso pode ser em decorrência do efeito direto das táticas de controle sobre *At. bondari*, mas também pode ser devido a menor presença de frutos infestados por *Ac. guerreronis*, que indiretamente afeta a infestação de *At. bondari* aos frutos de coqueiro. Todavia, em sistemas semi-extrativistas, representado em grande parte por áreas de produção da região do nordeste brasileiro (Martins & Jesus 2011), a mariposa é relatada com maior frequência nos frutos de coco (Ferreira *et al.* 2002).

Apesar de ocasionar necroses similares, não há estudo sobre o efeito da necrose causada por *S. concavuscutum* na infestação de *At. bondari*. Como as três espécies compartilham o mesmo local, a presença de uma ou de ambas as espécies de ácaros no fruto podem interferir distintamente na infestação das larvas de *At. bondari*. Santana *et al*. (2009) mostrou que *At. bondari* e *Ac. guerreronis* frequentemente co-ocorrem em frutos, no entanto, os autores não realizaram a avaliação dos frutos abortados. No caso de a infestação de *At. bondari* causar um maior abortamento de frutos não infestados por *Ac. guerreronis*, a associação observada no trabalho de Santana *et al*. (2009) pode ter sido superestimada pois a maioria dos frutos infestados apenas por *At. bondari* deveriam encontrar-se abortados. Os autores também não avaliaram a presença de *S. concavuscutum* nos frutos avaliados, e por compartilharem o mesmo local de alimentação, a herbioria de *S. concavuscutum* pode interferir na associação de *Ac. guerreronis* e *At. bondari*.

O sistema coqueiro-ácaro-mariposa foi novamente estudado, onde dessa vez foi inserido mais uma espécie de ácaro. Neste estudo foi realizado um levantamento de campo, mostrando como a distribuição de *At. bondari* dentro da palmeira é afeta pela presença ou ausência dos ácaros, além disso, verificou-se que o número de frutos abortados está correlacionado com a presença de *At. bondari*. Em laboratório foi avaliado como frutos não infestados e infestados por diferentes agentes (*Ac. guerreronis*, *S. concavuscutum* ou ambos os ácaros) interferem na habilidade das larvas de *At. bondari* em infestar os frutos do coqueiro. O tamanho do acesso à região meristemática de frutos não infestados e infestados por diferentes agentes (*Ac. guerreronis*, *S. concavuscutum*) foi estimado e comparado com a altura da capsula cefálica das larvas neonatas de *At. bondari*. Além disso, observou-se a preferência tanto das larvas neonatas de *At. bondari* por frutos não infestados e infestados por *Ac. guerreronis* e *S. concavuscutum*, quanto das das fêmeas adultas por cachos não infestados e infestados por *Ac. guerreronis* e *S. concavuscutum*. Finalmente foi avaliado se o desempenho das larvas neonatas de *At. bondari* é alterado quando alimentadas com frutos não infestados ou infestados por diferentes agentes (*Ac. guerreronis* ou *S. concavuscutum*).

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CHAPTER 2

WHICH SPECIES OF COCONUT MOTH OCCURS IN BRAZIL: *Atheloca subrufella* VS. *Atheloca bondari* (LEPIDOPTERA: PYRALIDAE)?[1]

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[1]Paz-Neto, A.A., M.T.S. Freitas, M.G.C. Gondim Jr., J.W.S. Melo, R.B. Querino & V.Q. Balbino. Which species of coconut moth occurs in Brazil: *Atheloca subrufella* vs. *Atheloca bondari* (Lepidoptera: Pyralidae)? Published in Neotropical Entomology.

ABSTRACT - The moths, *Atheloca subrufella* (Hulst 1887) and *A. bondari* (Heinrich 1956) are species known for their economic impact on coconut production, which Brazil is the fourth largest global producer. The first record of *Atheloca* in Brazil was performed by Bondar in 1940, which reported as being *A. subrufella*. The studies performed by C. Heinrich in 1956 related the existence of divergence in specimens of Brazilian Atheloca suggesting the presence of morphological differences between the males of *Atheloca bondari* and *Atheloca subrufella*. In this study, *Atheloca* specimens from five states from northeastern Brazil were used. Samples from Pernambuco state were sent to the taxonomist Dr. V.O. Becker (Uiraçu Institute-BA) for identification. Male from the other states were mounted for photographic documentation, highlighting the characteristics that differentiate the species. A fragment of the cytochrome c oxidase subunit 1 gene was sequenced and then compared to that of the *Atheloca* spp. deposited in GenBank. An analysis was conducted to evaluate the genetic distance relations between *A. bondari* and *A. subrufella*. The results indicate greater interspecific (0.030-0.034) than intraspecific (0.000-0.002) genetic variation between the groups, reinforcing the hypothesis of two distinct species. A geographic distribution map and a table with the host plants were constructed based on a literature review. We concluded that the species occurring in Brazil is *A. bondari*, as suggested by C. Heinrich. *Atheloca bondari* and *A. subrufella* have been reported in plants of the family Arecaceae, but only the coconut tree (*Cocos nucifera* L.) is shared by both.

KEY WORDS: DNA barcode, *Cocos nucifera*, integrative taxonomy, taxonomical errors

QUAL ESPÉCIE DE MARIPOSA DO COQUEIRO QUE OCORRE NO BRASIL: *ATHELOCA SUBRUFELLA* VS. *ATHELOCA BONDARI* (LEPIDOPTERA: PYRALIDAE)?

RESUMO – As mariposas *Atheloca subrufella* (Hulst 1887) e *A. bondari* (Heinrich 1956) são espécies conhecidas por seu impacto econômico na produção de coco, sendo o Brasil o quarto produtor mundial. O primeiro registro de Atheloca no Brasil foi realizado para Bondar em 1940, onde o autor registrou como *A. subrufella*. C. Heinrich em 1956 relatou divergência entre espécimes de Atheloca brasileira, destacando diferenças morfológicas entre os machos de *A. bondari* e *A. subrufella*. Neste estudo, foram utilizados espécimes de Atheloca de cinco estados do nordeste do Brasil. Amostras do estado de Pernambuco foram enviadas ao taxonomista Dr. V.O. Becker (Instituto Uiraçu-BA) para identificação. Indivíduos do sexo masculino dos demais estados foram montados para documentação fotográfica, destacando as características que diferenciam as duas espécies. Um fragmento do gene da subunidade 1 do citocromo c oxidase 1 foi sequenciado e depois comparado ao de *Atheloca* spp. depositados no GenBank. Uma análise foi realizada para avaliar as relações de distância genética entre *A. bondari* e *A. subrufella*. Os resultados indicam maior variação genética interespecífica (0,030-0,034) do que intraespecífica (0,000-0,002) entre os grupos, reforçando a hipótese de duas espécies distintas. Um mapa de distribuição geográfica e uma tabela com as plantas hospedeiras foram construídas com base em uma revisão da literatura. Este estudo concluiu que a espécie que ocorre no Brasil é *A. bondari*, conforme sugerido por C. Heinrich. *Atheloca bondari* e *A. subrufella* foram relatados apenas em plantas da família Arecaceae, mas apenas o coqueiro (*Cocos nucifera* L.) é compartilhado pelas duas espécies.

PALAVRAS-CHAVE: DNA barcode, *Cocos nucifera*, taxonomia integrativa, erro taxonômico

Introduction

The genus *Atheloca* Heinrich belongs to the subfamily Phycitinae and is formed by two unique species: *Atheloca subrufella* (Hulst 1887) and *Atheloca bondari* (Heinrich 1956). *Atheloca subrufella* has been reported in the United States, Cuba, US Virgin Islands (Heinrich 1956, Cock & Burris 2013), Costa Rica (http://www.boldsystems.org/), and Brazil (Bondar 1940). In turn, the occurrence of *A. bondari* has been restricted to date in only three countries: Trinidad and Tobago (Cock & Burris 2013), Colombia (http://www.boldsystems.org/), and Brazil (Heinrich 1956).

Bondar (1940) reported the occurrence of *A. subrufella* in the state of Bahia in Brazil, on inflorescences of coconut trees (*Cocos nucifera* L.) and native palm trees of the genera *Attalea* (Kunth) and *Syagrus* Martius. Bondar's report was based on type materials collected in the United States and Cuba, where *A. subrufella* was the only known species of the genus. Subsequently, Heinrich (1956) performed a review of all known species of the subfamily Phycitinae occurring in the New World. In studying the material collected by G.G. Bondar, deposited in the United States National Museum (USNM, 61335), Heinrich noticed that the hind tibia of Brazilian male specimens had tufts of long scales, a characteristic not found in individuals in the United States, Cuba, and the US Virgin Islands. Heinrich decided to describe a new taxon (*A. bondari*) to represent the species occurring in Brazil. Currently, the studies carried out in Brazil with the species of *Atheloca* tend to disregard the data from Heinrich (1956).

Atheloca has been the focus of recent studies in Brazil (Bento *et al*. 2006, Sarro *et al*. 2007, Santana *et al*. 2009, 2010a, 2010b, Nascimento *et al.* 2016), and taxonomic references cited in these studies seem to be taken from Bondar (1940) and Gallo *et al*. (2002), contributing to the dissemination of information that indicates the taxon that occurs in Brazil is *A*. *subrufella* and not *A. bondari*. None of the studies conducted in Brazil reference the study that separates *A. subrufella* from *A. bondari* (Heinrich 1956). Cock & Burris (2013) reported this possible taxonomic confusion between congeneric species and cited a personal communication from M.A. Solis (Phycitinae taxonomist) about the possibility of these species being synonyms. However, no studies have investigated this topic thus far, and the names of both species remain valid (Beccaloni *et al*. 2003).

The present study aimed to define the identity of the taxa of Atheloca species that occur in northeastern Brazil. Due to little morphological variability between the two species, we used integrative taxonomy (Dayrat 2005), where a taxonomist is responsible for morphological analysis, which is then complemented by molecular tools (barcode DNA).

Materials and Methods

Field collection and laboratory rearing of adult *Atheloca*. Aborted fruits of *C. nucifera* were collected in the field, with only those that had excrement connected by silk threads on the surface of the fruit, which is an indication of the presence of *Atheloca* larvae, being collected. Samplings were carried out in the following locations: Nísia Floresta/Rio Grande do Norte-RN site 1 (6°3'S, 35°6'W), Nísia Floresta/RN site 2 (6°6'S, 35°10'W), Rio Tinto/Paraíba-PB (6°46'S, 35°1'W), Jacumã/PB (7°16'S, 34°49'W), Pitimbu/PB (7°31'S, 34°49' W), Itamaracá/Pernambuco-PE (7°48'S, 34°50'W), Barra de Sirinhaém/PE (8°39'S, 35°4'W), Maragogi/Alagoas-AL (8°59'S, 35°12'W), Feliz Deserto/AL (10°20'S, 36°19'W) Pirambu/Sergipe-SE (10°42'S, 36°51'W) and Aracaju/SE (10°57'S, 37°2'W). Sampling was carried out in each location, with approximately 30 fruits of different ages being collected. Then, the fruits were stored in labeled plastic bags and transported to the Laboratory of the Federal Rural University of Pernambuco (UFRPE) and stored at room temperature for 24 h until the samples were processed.

At laboratory, each fruit had its bracts carefully removed to larvae collection, which were placed in infestation-free fruits obtained from the UFRPE campus (8°0'S, 34°56'W), according to the methodology developed by Santana *et al*. (2010b). A scalpel was used to make cuts in the epidermis of the fruit; a triangular opening (0.5 cm per side), was created just below the bracts, where the larvae were introduced. The fruits were placed in a Styrofoam holder to keep them in an upright position and then were placed inside clear plastic cages measuring 12 × 17 cm (diameter and height) and containing lateral openings covered with voile fabric. At the end of development, the larvae emerged from the fruit and pupated on a paper towel placed inside the cage as a substrate. The pupae were removed and placed in acrylic bottles (2.0 × 3.5 cm) until adult emergence.

Taxonomic identification

Morphological identification. Eighteen adults (males and females) from the municipality of Itamaracá/PE were mounted with micropins and sent to the microlepidoptera taxonomy specialist Dr. Vitor Osmar Becker (Uiraçu Institute-BA) for identification. The genitalia of the males were mounted and compared with the genitalia of *A. subrufella* drawn by G.D. Hulst and referenced in Heinrich's thesis (1956). The voucher specimens were deposited in V.O. Becker's personal collection. The individuals from the other locations were mounted with micropins to allow analysis of the morphological characteristic that differentiate the two species. Then, all subjects were labeled, photographed and stored in entomological boxes in the Acarology Laboratory of UFRPE. We used the software Photoshop CS6® to edit the photos.

Molecular identification. Specimens from the Itamaracá/PE collection were used for genetic characterization, using DNA barcoding. Five adults were preserved in 90% ethanol and refrigerated (°C) until the analyses were performed. The genomic DNA was extracted with Chelex®100 (BioRad, Berkeley, California, USA), according to methodology employed by Costa *et al*. (2015). Degenerate primers specific for insects, namely, HCO2198-L (5'-TAAACTTCWGGRTGWCCAAARAATCA-3') and LCO1490-L (5'-

GGTCWACWAATCATAAAGATATTGG-3') (Nelson *et al.* 2007), were used to amplify a fragment of the cytochrome c oxidase subunit I gene (*COI;* ~578 bp) of the mitochondrial genome (mtDNA).

Amplification was performed with the GoTaq® Colorless Master Mix, according to the manufacturer's instructions (Promega, Fitchburg, Wisconsin, USA). PCR products were visualized on 1% agarose gel under UV light and purified with a Gel Wizard® SV and PCR Cleaning System (Promega, Fitchburg, Wisconsin, USA).

Sequencing was performed on the ABI 3500 automated sequencer (Applied Biosystems, Cleveland, Ohio, USA). Only sequences with a Phred score (Ewing *et al.* 1998) above 30 were used in the analyses. The contig assembly was performed using the CodonCode Aligner (CodonCode Corporation). The sequences amplified in this study were compared regarding identity in the Barcode of Life Data Systems (BOLD) for *A. bondari* (LNAUU046-15) and *A. subrufella* (BBLOB412-11, BBLOB419-11, BBLOB426-11, and BBLOB425-11), and the local alignments were performed using BLASTtn (Altschul *et al.* 1990). All new sequences produced in this study were deposited in GenBank under GenBank numbers MF973050 to MF973054.

Subsequently, the sequences were aligned using MUSCLE (Edgar 2004), incorporated into the MEGA v. 6.0 software (Tamura *et al*. 2011). Genetic distance analysis was performed using the neighbor-joining clustering method (Saitou & Nei 1987) and Kimura's two-parameter (K2P) nucleotide substitution model (Kimura 1980) in the MEGA software (Tamura *et al*. 2011). Branch robustness was evaluated using 1,000 bootstrap replicates. The sequences obtained in BOLD databases for *A. bondari* (LNAUU046-15) and *A. subrufella* (BBLOB412-11, BBLOB419-11, BBLOB426-11 and BBLOB425-11) were used for comparison of genetic distance relations (Table 1).

The degree of genetic divergence among the individuals was also analyzed using intraspecific and interspecific distance through the K2P distance matrix (Kimura 1980) implemented in MEGA v. 6.0 (Tamura *et al*. 2011).

Geographical distribution and host plants. A literature review was carried out on the databases from the following sites: http://www.nhm.ac.uk/our-science/data/hostplants/; http://globiz.pyraloidea.org; http://www.boldsystems.org/; https://www.butterfliesandmoths.org/; and data from articles by Bondar (1940), Heinrich (1956), Habeck and Nickerson (1982), and Cock and Burris (2013). The geographical distribution map and a table containing the host plants of both species were created with the surveyed data. The map was created through the site https://www.simplemappr.net/.

Results

Taxonomic identification

Morphological identification. Visual analysis of the genitalia of the males from Itamaracá-PE showed no differences among the specimens of this study and the species *A. subrufella.* This result is expected since Heinrich (1956) reported no differences between the genitalia of the two *Atheloca* species. However, Dr. V.O. Becker reports the presence of tufts of long yellow scales on the hind tibia of the studied males, previously identified as being *A. bondari*, as suggested by Heinrich (1956). Male specimens collected in all locations in this study show the same characteristic (tufts of long yellow scales in the hind tibia of the males) that morphologically separates *A. bondari* from *A. subrufella* (Fig. 1).

Molecular identification. The comparison of the sequences obtained in this study with sequences found in the Barcode of Life Data Systems (BOLD) showed identity values between 98 and 99% for *A. bondari*. Genetic distance analyses suggest a relevant divergence between the specimens evaluated, revealing two groups supported by 100% bootstrap values (Fig. 2). The K2P distance matrix values (Table 2) indicate greater interspecific (0.030-0.034) than intraspecific (0.000-0.002) genetic variation.

Geographical distribution and host plants. *Atheloca bondari* has been recorded in Brazil, Trinidad and Tobago, and Colombia; *A. subrufella,* in the United States, Caribbean Islands (Cuba, US Virgin Islands), and Costa Rica (Fig. 3). *Atheloca bondari* occurs in *Attalea piassabossu* (Bondar), *Attalea funifera* (Mart.), *Syagrus vagans* (Bondar), *Syagrus coronata* (Mart.), and *Roystonea oleracea* (Jacq.), whereas *A. subrufella* occurs in *Sabal palmetto* (Walt.) and *Serenoa repens* (Bartram). *Cocos nucifera* is the only host palm tree common to both species (Table 3).

Discussion

The results of the morphological identification carried out by the taxonomist V.O. Becker on the specimens of the municipality of Itamaracá-PE indicate that these individuals belong to the species *A. bondari* because the males had tufts of long, yellow scales on the hind tibia. This was the characteristic used by Heinrich (1956) to separate *A. bondari* from *A. subrufella*. In the study by Bondar (1940), the photographic documentation of the individuals was not conducted, making comparison impossible. The males from all locations sampled in this study have long scales on the hind tibia (Fig. 1), indicating that the species occurring in northeastern Brazil is *A. bondari* and not *A. subrufella*, as suggested by Heinrich (1956).

The *COI* fragment sequences produced in this study show that when the sequences of the collected individuals are compared to other sequences deposited in GenBank, the individuals are genetically similar to the species *A. bondari* (98-99%). Genetic distance analyses indicate an important divergence between the two *Atheloca* species, revealing two distinct groups (*A. subrufella* and *A. bondari*) that are well supported by bootstrap values of 100%.

Although the two *Atheloca* species are recognized as agricultural pests (Bondar 1940, Habeck & Nickerson 1982), few records exist in the literature for *A. bondari* and *A. subrufella*. The few reports available show that, thus far, no overlap exists in the geographic distribution of *A. bondari* and *A. subrufella*, as indicated by the distribution map of the species (Fig. 3). *Atheloca bondari* has been reported in Brazil, Trinidad and Tobago, and Colombia, while *A. subrufella* occurs in the United States, the Caribbean Islands (Cuba and the US Virgin Islands), and Costa Rica (Bondar 1940, Heinrich 1956, Cock & Burris 2013, http://www.boldsystems.org/).

In the current literature, *A. subrufella* is reported as occurring in Brazil; however, all studies that make such reports cite Bondar (1940), disregarding Heinrich's review (1956). In Santana's thesis (2008), for example, the species studied was determined to be *A. bondari* due to photographic documentation of the hind leg of the male; however, no photographic record of this trait was found in the other studies (see Bondar 1940, Bento *et al*. 2006, Sarro *et al*. 2007, Nascimento *et al*. 2016). Due to the evidence found in that study, all records in the Brazilian territory belong to *A. bondari*.

The literature review shows few host species for *A. bondari* and *A. subrufella*; however, this finding may reflect the rarity of the papers that record their hosts (Bondar 1940, Kimball 1965, Habeck & Nickerson 1982, Cock & Burris 2013). Only plants of the family Arecaceae are identified as hosts of *A. bondari* and *A. subrufella*; however, only the coconut palm, which is an exotic palm of the American Continent, is a host shared by both species. In addition to being reported on the coconut palm, *A. bondari* was recorded on inflorescences of *A. funifera*, *A. piassabossu*, *R. oleracea, S. coronata* and *S. vagans*, native palms of Central and South America, while *A. subrufella* was recorded in inflorescences of *S. palmetto* and *S. repens*, palms native to North America. Apparently, this host differentiation among palm trees native to the American continent reinforces the geographic zoning of the *Atheloca* species.

Packer *et al*. (2018) has some important suggestions that should be considered to prevent the dissemination of taxonomic errors in applied studies, such as clearly indicating the reference used in identification, highlighting the taxonomist responsible for the identification, and the deposit of voucher specimens. The arguments highlighted by Packer *et al*. (2018) are extremely relevant and could have avoided the dissemination of doubt about the identity of the *Atheloca* species occurring in Brazil.

This study provides evidence of the existence of two species within the genus *Atheloca* and indicates that the species occurring in northeastern Brazil is *A. bondari*.

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Table 1. Information of each Atheloca species barcode sequence used in this study.

Accession Number|Species	Country	Databases
BBLOB412-11|*A.subrufella*|COI-5P	United States	BOLD
BBLOB419-11|*A.subrufella*|COI-5P	United States	BOLD
BBLOB426-11|*A.subrufella*|COI-5P	United States	BOLD
BBLOB425-11|*A.subrufella*|COI-5P	United States	BOLD
LNAUU046-15|*A.bondari*|COI-5P	Colombia	BOLD
MF973054|ITAMARACA-PE_01	Brazil	GenBank
MF973053|ITAMARACA-PE_02	Brazil	GenBank
MF973052|ITAMARACA-PE_03	Brazil	GenBank
MF973051|ITAMARACA-PE_04	Brazil	GenBank
MF973050|ITAMARACA-PE_05	Brazil	GenBank

Table 2. Pairwise distances between samples using Kimura two-parameter model.

	1	2	3	4	5	6	7	8	9	10
1.BBLOB412-11|*A.subrufella*|COI-5P	0.000									
2.BBLOB419-11|*A.subrufella*|COI-5P	0.000	0.000								
3.BBLOB426-11|*A.subrufella*|COI-5P	0.000	0.000	0.000							
4.BBLOB425-11|*A.subrufella*|COI-5P	0.002	0.002	0.002	0.000						
5.LNAUU046-15|*A.bondari*|COI-5P	0.034	0.034	0.034	0.032	0.000					
6.ITAMARACA-PE_01	0.032	0.032	0.032	0.030	0.002	0.000				
7.ITAMARACA-PE_02	0.032	0.032	0.032	0.030	0.002	0.000	0.000			
8.ITAMARACA-PE_03	0.032	0.032	0.032	0.030	0.002	0.000	0.000	0.000		
9.ITAMARACA-PE_04	0.032	0.032	0.032	0.030	0.002	0.000	0.000	0.000	0.000	
10.ITAMARACA-PE_05	0.032	0.032	0.032	0.030	0.002	0.000	0.000	0.000	0.000	0.000

Table 3. Diversity of host plants of *Atheloca bondari* and *Atheloca subrufella*.

Species	Host Plant	Reference
A. bondari	*Cocos nucifera*	Bondar (1940); Cock & Burris (2013); (this survey)
A. bondari	*Roystonea oleracea*	Cock & Burris(2013)
A. bondari	*Syagrus coronata*	Bondar (1940)
A. bondari	*Syagrus vagans*	Bondar (1940)
A. bondari	*Attalea funifera*	Bondar (1940)
A. bondari	*Attalea piassabossu* (*A. funifera* X *A. oleifera*)	Bondar (1940)
A. subrufella	*Cocos nucifera*	Habeck & Nickerson (1982)
A. subrufella	*Sabal palmetto*	Kimball (1965)
A. subrufella	*Serenoa repens*	Kimball (1965)

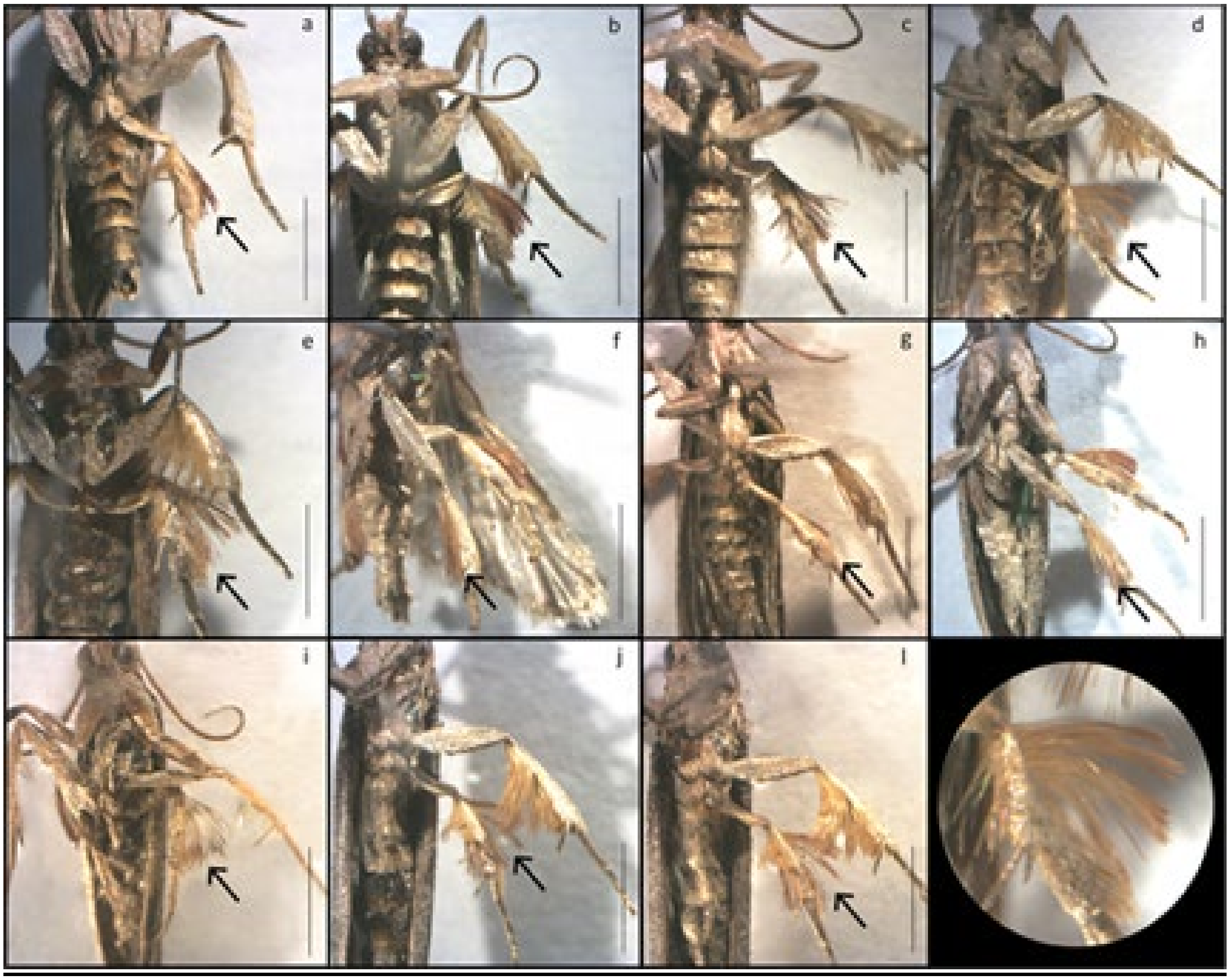

Figure 1. Photographic record of the males of *Atheloca bondari*. (A) Nisia Floresta/RN 1; (B) Nísia Floresta/RN 2; (C) Rio Tinto/PB; (D) Jacumã/PB; (E) Pitimbu/PB; (F) Itamaracá/PE; (G) Barra de Sirinhaém/PE; (H) Maragogi/AL; (I) Feliz Deserto/AL; (J) Pirambu/SE; (L) Aracaju/SE. Scale standardized to 2.5 cm. Arrows indicate the presence of long scales on the hind tibia.

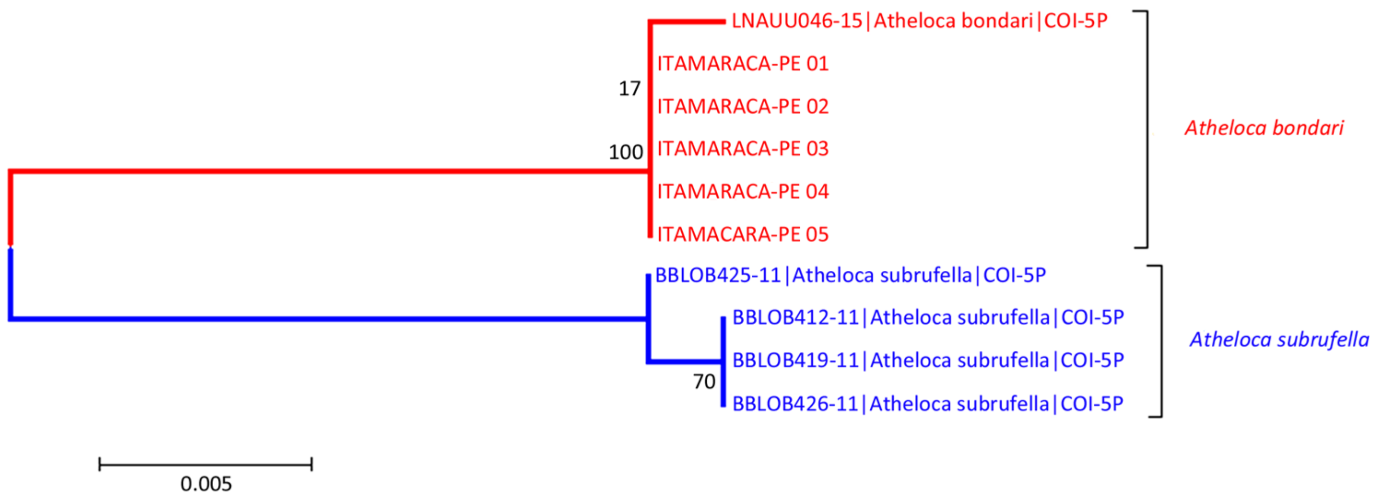

Figure 2. Genetic distance analysis of *Atheloca subrufella* and *Atheloca bondari* specimens using cytochrome oxidase I (*COI*). A neighbor-joining tree was generated with Kimura's two-parameter model and 578 bp of *COI* sequences.

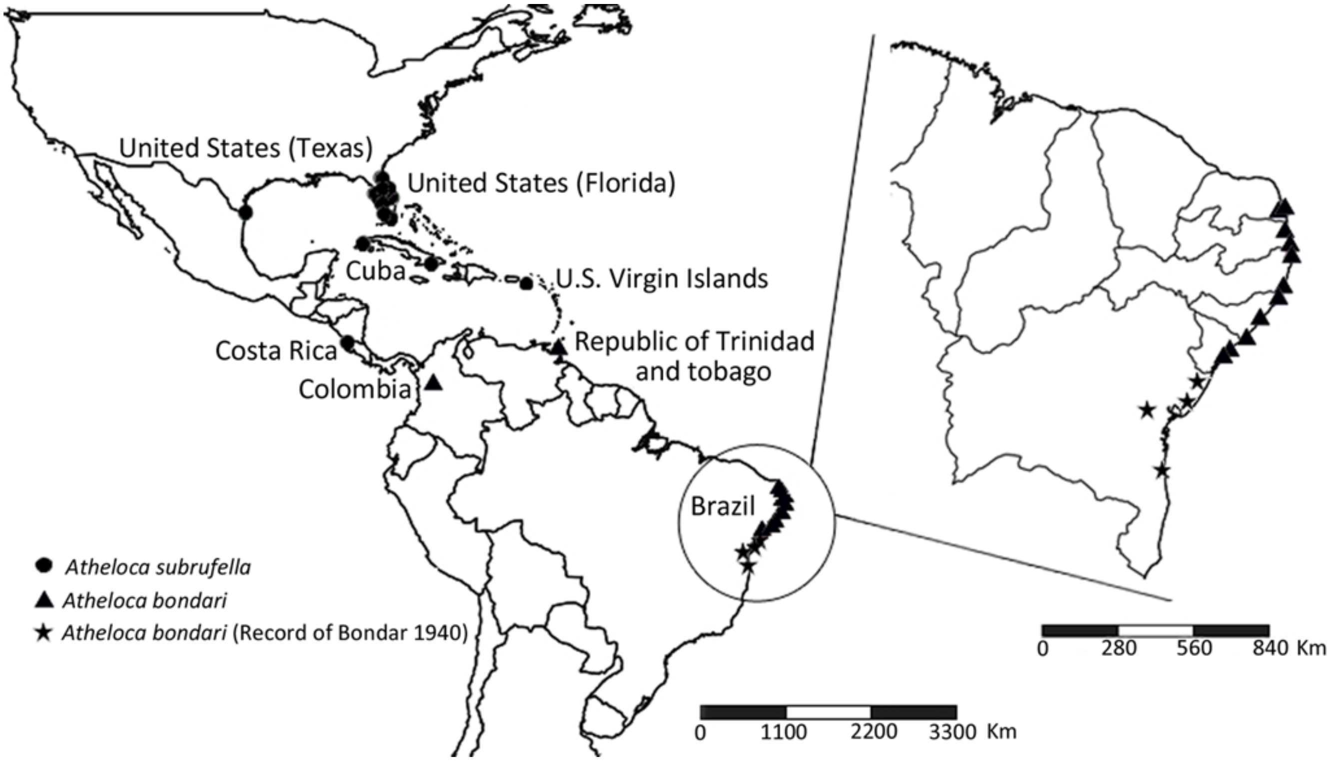

Figure 3. Geographical distribution map of *Atheloca bondari* and *Atheloca subrufella*. Stars represent the sites where Bondar (1940) recorded the occurrence of *Atheloca subrufella,* corrected here to *Atheloca bondari*.

CHAPTER 3

FIELD DISTRIBUTION PATTERNS OF PESTS ARE ASYMMETRICALLY AFFECTED BY THE PRESENCE OF OTHER HERBIVORES[1]

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[1] Paz-Neto, A.A., J.W.S. Melo, D.B. Lima, M.G.C. Gondim Jr. & A. Janssen. Field distribution patterns of pests are asymmetrically affected by the presence of other herbivores. Accepted by Bulletin of Entomological Research.

ABSTRACT **-** Because plant phenotypes can change in response to attacks by herbivores in highly variable ways, the distribution of herbivores depends on the occurrence of other herbivore species on the same plant. We carried out a field study to evaluate the co-occurrence of three coconut pests, the mites *Aceria guerreronis* (Acari: Eriophyidae), *Steneotarsonemus concavuscutum* (Acari: Tarsonemidae) and the moth *Atheloca bondari* (Lepidoptera: Pyralidae). The eriophyid mite *Ac. guerreronis* is the most important coconut pest around the world, whereas *S. concavuscutum* and *At. bondari* are economically important only in some areas along the Brazilian coast. A previous study suggested that the necrosis caused by *Ac. guerreronis* facilitates the infestation of *At. bondari* larvae. Because all three species infest the area under the perianths on coconuts and *S. concavuscutum* also causes necrosis that could facilitate *At. bondari*, we evaluated the co-occurrence of all three species. We found that the occurrence of *At. bondari* was positively associated with *Ac. guerreronis*, but negatively associated with *S. concavuscutum*. In addition, the two mite species showed negative co-occurrence. *Atheloca bondari* was found on nuts of all ages, but more on nuts that had fallen than on those on the trees, suggesting that nuts infested by *At. bondari* tend to fall more frequently. We discuss the status of *At. bondari* as a pest and discuss experiments to test the causes of these co-occurrence patterns.

KEY WORDS: *Cocos nucifera*, facilitative occurrence, indirect interaction, mite-insect-plant association, plant-trait indeuced by herbivory

O PADRÃO DE DISTRIBUIÇÃO DE PRAGAS NO CAMPO É AFETADO ASSIMETRICAMENTE PELA PRESENÇA DE OUTROS HERBÍVOROS

RESUMO – Como os fenótipos de plantas podem mudar em resposta a ataques de herbívoros de maneiras altamente variáveis, a distribuição de herbívoros depende da ocorrência de outras espécies de herbívoros na mesma planta. Realizamos um estudo de campo para avaliar a co-ocorrência de três pragas de coco, os ácaros *Aceria guerreronis* (Acari: Eriophyidae), *Steneotarsonemus concavuscutum* (Acari: Tarsonemidae) e a mariposa *Atheloca bondari* (Lepidoptera: Pyralidae). O ácaro eriófídeo *A. guerreronis* é a praga de coco mais importante do mundo, enquanto *S. concavuscutum* e *A. bondari* são economicamente importantes apenas em algumas áreas ao longo da costa brasileira. Um estudo anterior sugeriu que a necrose causada por *A. guerreronis* facilita a infestação de larvas de *A. bondari*. Como as três espécies infestam a área sob os periantos dos cocos e *S. concavuscutum* também causa necrose que pode facilitar *A. bondari*, avaliamos a co-ocorrência das três espécies. Verificamos que a ocorrência de *A. bondari* foi associada positivamente a *A. guerreronis*, mas negativamente associada a *S. concavuscutum*. Além disso, as duas espécies de ácaros apresentaram co-ocorrência negativa. *Atheloca bondari* foi encontrado em frutos de todas as idades, mas com maior ocorrência em frutos que abortaram das palmeiras, sugerindo que os frutos infestados por *A. bondari* tendem a abortar com mais frequência. Discutimos o status de *A. bondari* como uma praga e sugerimos experimentos para testar as causas desses padrões de co-ocorrência.

PALAVRAS-CHAVE: *Cocos nucifera*, ocorrência facilitada, interação indireta, associação ácaro-inseto-planta, características das plantas induzidas por herbivoria

Introduction

Biotic interactions play an important role in the structure and stability of ecological communities (Ives & Carpenter 2007, Thébault & Fontaine 2010, Benkman 2013). Food web interactions have been extensively investigated in ecological research (Williams & Martinez 2000, Tang *et al*. 2014, Allesina *et al*. 2015), showing that direct trophic (feeding) interactions are only one of many mechanisms by which species can influence each other (Bertness & Callaway 1994, Ings *et al*. 2009, Mougi & Kondoh 2012, Sanders *et al*. 2014), and that non-trophic interactions can have important effects on the dynamic of insect populations (Schmitz 1998, Anderson *et al*. 2009, Utsumi 2011). Both trophic and non-trophic interactions can change species distribution and abundance through trait- and density-mediated indirect effects (Ohgushi *et al*. 2007, Bukovinszky *et al*. 2008, Eubanks & Finke 2014). Indirect effects occur when the effect of one species on another is mediated by changes to a third species (Wootton 1994).

Trait-mediated indirect interactions are important in plant-insect communities (Ohgushi 2008, Karban 2011, Giron *et al*. 2018) because herbivory leads to phenotypic changes affecting physiology, chemistry and morphology of the plant (Karban & Baldwin 1997, Kant *et al*. 2015, Ohgushi & Hambäck 2015), which affect the performance of other herbivores. These herbivore-induced plant traits have the potential to affect whole host plant communities (Dicke *et al*. 2009, Soler *et al*. 2012, Poelman & Kessler 2016, Stam *et al*. 2018, Vaello *et al*. 2018), and they may facilitate or impede the performance of subsequent herbivores (Stam *et al*. 2014, Harvey *et al*. 2015, Cornelissen *et al*. 2016, Uesugi *et al*. 2016, Lee *et al*. 2017, Li *et al*. 2018). Changes caused by herbivory can create new habitats within a plant that can be used by opportunistic herbivores (Ohgushi 2008). Plants are often attacked by multiple herbivores and they respond specifically to single or dual herbivory (Kessler & Halitschke 2007, Poelman *et al*. 2008), which differentially affects the interactions with a third herbivore (Kroes *et al*. 2016). Here, we studied a special case of an interaction among herbivores, wherein the natural distribution of the moth *Atheloca bondari* Heinrich (Lepidoptera: Pyralidae) is influenced by the co-occurrence with the mites *Aceria guerreronis* Keifer (Acari: Eriophyidae) and *Steneotarsonemus concavuscutum* Lofego and Gondim Jr. (Acari: Tarsonemidae). Assessing this co-occurrence is a first step in assessing the pest status of this moth as a coconut pest in natural fields.

The coconut palm is a perennial plant native to Southeast Asia but is currently distributed throughout the pantropics (Chan & Elevitch 2006, Gunn *et al*. 2011, Ahuja *et al*. 2014) and considered a crop of economic importance in many countries (Hoe 2018). Mites and months are considered important coconut pests around the world, usually related to decreasing production of coconut fruits due to damage and abortion of the reproductive structure (Bondar 1940, Moore *et al*. 2001, Aratchige 2010, Navia *et al*. 2013, Rezende *et al*. 2016). Larvae of different species of moths feed on the male and female flowers of coconuts (Bondar 1940, Moore *et al*. 2001, Cock & Burris 2013). The moths can complete their life cycle in developing nuts (Bento *et al*. 2006, Santana *et al*. 2010), but their occurrence in nuts is very low. This suggests that the larvae of moths are not able to bore the exocarp of the nuts.

The exterior of the nut is formed by a fibrous exocarp and an arranged set of tepals (perianths) covering the meristematic region (Smit 1970, Howard & Rodriguez 1991). Herbivores that can access the meristematic region can feed on nutritional tissues, but only very small organisms such as mites are able to enter the space between the exocarp and perianth (Moore *et al*. 2001, Navia *et al*. 2005, Lawson-Balagbo *et al.* 2008). For example, the mites *Ac. guerreronis* and *S. concavuscutum* are often found feeding on the meristematic region of the nuts under the perianth (Lofego & Gondim Jr. 2006, Lawson-Balagbo *et al*. 2007, Lima *et al*. 2017). Coconuts infested by mites show necrotic lesions extending from the meristematic region to the surface of the nut not covered by the perianth (Navia *et al*. 2005, Lofego & Gondim Jr. 2006).

A previous study shows that the moth *At. bondari* is an opportunistic species that uses necrosis of *Ac. guerreronis* to access the meristematic region of the nut (Santana *et al.* 2009). Although *At. bondari* is associated with economic loss in coconut crops (Bondar 1940, Ferreira *et al*. 2002), the study of Santana *et al*. (2009) reveals that this species may be a secondary pest. However, Santana *et al*. (2009) did not evaluate fallen nuts, and if nuts infested only by *At. bondari* have a higher probability of falling, the co-occurrence between *At. bondari* and *Ac. guerreronis* may have been overestimated.

In the laboratory, larvae of *At. bondari* were better able to access the meristematic region of nuts that had necrosis of *Ac. guerreronis* or had received mechanical damage (Santana *et al*. 2009), reinforcing the idea that morphological changes of the exocarp of the coconut facilitates the infestation of the larva of *At. bondari*. *Aceria guerreronis* and *S. concavuscutum* cause similar necrotic lesion patterns (Navia *et al*. 2005), so it is expected that *At. bondari* also co-occurs with *S. concavuscutum*. This is what we set out to test in this manuscript by sampling coconuts in the field and assessing co-occurrence of the moth and the two mite species.

Since the space between the perianth and the exocarp increases as fruits ages (Lima *et al*. 2012), we collected nuts with different ages to analyse if age influenced the occurrence of *At. bondari* larvae. In addition, as both mite species and the moth occupy the same feeding sites, thus, each could in theory influence the distribution of the other species (Capitán *et al*. 2015, Segre *et al*. 2016), we also evaluated the co-occurrence of the mites and how this influenced the presence of *At. bondari*.

Materials and Methods

We randomly collected bunches from the tree and fallen nuts of coconut palms (*Cocos nucifera* L.). According to coconut tree phyllotaxis (Sobral 1994), we collected the bunches corresponding to leaves 12-16, which refers to bunches of 2 to 6 months old, respectively. The fallen nuts under the palm trees were collected, the age of fallen nuts was determined by comparing their size with nuts removed from bunches of the palm tree, and fallen nuts were subsequently grouped by age. Fallen nuts that did not have the perianths or that were damaged by humans were not evaluated. Nuts were harvested from trees every 15 days in the state of Pernambuco, Brazil, between March and July of 2016 in the following fields: Itamaracá (Sossego) (7°43' S, 34°49' W), Itamaracá (Pilar) (7°47' S, 34°51' W), Itamaracá (Coroa do Avião) (7°48' S, 34°50' W) and Igarassú (Mangue Seco) (7°49' S, 34°50' W). Fallen nuts were collected only from Igarassú (Mangue Seco). In total, 1194 nuts (967 collected from coconut palms and 227 fallen nuts) were brought to the laboratory for evaluation, where we carefully removed the perianths and observed the meristematic region under them with a stereomicroscope (Zeiss Stemi DV4), and we scored the presence of *Ac. guerreronis*, *S. concavuscutum* and larvae of *At. bondari*.

The probability of co-occurrence was calculated following Griffith *et al.* (2016), assuming a hypergeometric distribution:

$$Pj = \frac{\binom{N_1}{j} \times \binom{N-N_1}{N_2-j}}{\binom{N}{N_2}},$$

with N_i the number of nuts with species i (= 1, 2) and N the total number of plants sampled, and j ranging from 1 to N_1 (Griffith *et al.* 2016). This probability shows whether the species are positively, negatively or randomly associated. We analysed all co-occurrence combinations among species and discuss the results with a focus on *At. bondari* infestations. A positive association could be the result of attraction of *At. bondari* and the mites to the same nuts, independent of the presence of the other species or of facilitation of the caterpillars entering the area under the perianth due to mite damage. The absence of a positive or negative association would show that the moths and mites are not attracted to the same nuts, and that the infestation of mites does not facilitate the infestation by moths. The proportions of nuts infested by the different herbivores were compared between fallen nuts and nuts on trees and among nuts of different ages with a generalized linear model (GLM) with a binomial error distribution (Crawley 2013). All statistical analyses were performed in R (R Development Core Team 2014).

Results

The presence of *At. bondari* larvae in nuts not infested by mites was lower than expected in both fallen fruits and fruit from trees (Fig. 1,2). We observed a significant positive co-occurrence between *At. bondari* and *Ac. guerreronis* in both nuts collected from coconut palms and in fallen nuts (Fig. 1,2). The moth occurred significantly less than expected when the nuts on trees were infested by *S. concavuscutum* (Fig. 1), but the numbers of fallen fruits coinfested with *At. bondari* and *S. concavuscutum* did not differ from expected under a random distribution (Fig. 2). The observed distribution of *At. bondari* also did not differ from expected for nuts infested by both species of mites, both in nuts from trees and in fallen nuts (Fig. 1,2). Furthermore, we found that *Ac. guerreronis* and *S. concavuscutum* co-occur less than expected in nuts from trees and fallen nuts (Fig. 1,2).

The distance between the edge of the perianth of coconut and the subjacent nut surface increases with nut age (Lima *et al*. 2012) and may therefore become more accessible to the moth caterpillars. We therefore first analysed the occurrence of *At. bondari* in nuts of different ages both in fallen nuts and nuts from trees. The proportion of *At. bondari* did not differ among nuts of different ages ($P = 0.32$), but the proportion of infested nuts was higher in fallen nuts than from trees ($P < 0.0001$) (Fig. 3).

Third, we analysed the co-occurrence of *At. bondari*, *Ac. guerreronis* and *S. concavuscutum* in nuts of different ages. The proportion of *At. bondari* was higher than expected in nuts infested by *Ac. guerreronis* of all ages sampled from coconut palm (Fig. 4a). The proportion of fallen nuts infested by *At. bondari* and *Ac. guerreronis* was also higher than expected at all ages sampled, however this difference was not always significant (Fig. 4b).

The proportion of nuts infested by *At. bondari* and *S. concavuscutum* varied between different ages. In nuts collected from palm trees, the co-occurrence of these two species was lower than expected at age 3, age 4 and age 5 (Fig. 4c). The co-occurrence of *At. bondari* and *S. concavuscutum* did not differ from expected on fallen fruits of any age (Fig. 4d).

Co-occurrence of the three species did not differ from random in nuts of different ages. In nuts collected from trees, *At. bondari*, *Ac. guerreronis* and *S. concavuscutum* co-occurred more often than expected only in nuts of age 2 (Fig. 5e). There was no difference in occurrence in fallen nuts of any age (Fig. 5f).

Co-occurrence of the two mites was significantly lower than expected for all nut ages both on nuts collected from coconut palm and on fallen nuts. In nuts from trees, the proportion of nuts infested by *Ac. guerreronis* and *S. concavuscutum* did not differ from expected at age 2 (Fig. 5g). In fallen nuts, the co-occurrence of mites was significantly lower than expected at age 3, age 4 and age 6 (Fig. 5h).

Finally, we compared the occurrence and co-occurrence of species between fruits collected from trees and fallen fruits. The proportion of fruits with *At. bondari* was always higher in fallen fruits than fruits from trees, but the proportion of fruits infested by *At. bondari* together with *S. concavuscutum* did not differ between fruit origins (Fig. 6a, b, c). The proportion of fruits infested by *At. bondari* and *Ac. guerreronis* was significantly higher in fallen fruits than in fruits from trees, but the proportion of fruits infested by *Ac. guerreronis* without *At. bondari* was higher in fruits from trees than in fallen fruits (Fig. 6a). The proportion of fruits infested by *At. bondari* without *Ac. guerreronis* was higher in fallen fruits (Fig. 6a). The highest proportion of fruits without these two species was found in fruits collected from the palm trees (Fig. 6a).

Steneotarsonemus concavuscutum occurred more in fruits collected from trees than in fallen fruits when not co-occurring with *At. bondari* (Fig. 6b). In contrast, without *S. concavuscutum*, *At. bondari* occurred significantly more in fallen fruits. The proportion of fruits without these two species was higher in fruits collected from the trees (Fig. 6b).

The proportion of fruits infested by both mites without *At. bondari* was higher in fruits from trees than in fallen fruits, the same was found for fruits without any of the three species (Fig. 6c). The occurrence of *At. bondari* in fruits not infested by mites was higher in fallen fruits than fruits from coconut palms (Fig. 6c).

Without *S. concavuscutum*, *Ac. guerreronis* was observed in higher proportions in fallen fruits than in fruits from trees, this is probably due to the higher co-occurrence of *At. bondari* with *Ac. guerreronis* (Fig. 6d).

Discussion

We show positive and negative co-occurrence among three species that use coconuts as a resource. The occurrence of larvae of the moth *At. bondari* under the perianths of coconuts on palm trees was higher than expected when the nuts were infested by *Ac. guerreronis*, whereas it was lower than expected for nuts that were infested by the other mite species *S. concavuscutum* (Fig. 1). Santana *et al*. (2009) suggest that the co-occurrence of *At. bondari* and *Ac. guerreronis* is mainly due to a change in nut shape caused by the necrotic lesions of the mite, which allow the larvae of the moth access to the meristematic region under the perianths. However, the patterns of necrotic lesions caused by *S. concavuscutum* are similar to those caused by *Ac. guerreronis* (Navia *et al*. 2005), thus positive co-occurrence would also be expected between *S. concavuscutum* and *At. bondari*. Thus, our results show that the co-occurrence among these species seems not to be related only to the necrotic lesions caused by the mites.

Another explanation for the co-occurrence, or lack thereof, is the effects of the herbivores on each other through induced plant defences. Changes of plant traits induced by herbivory (Karban & Baldwin 1997, Kessler & Baldwin 2002, Kant *et al*. 2015) are known to affect the interactions in herbivore-plant communities (Gouinguené & Turlings 2002, Heil 2008, Ohgushi 2008, Ali & Agrawal 2014, Stam *et al*. 2014, Ohgushi & Hamback 2015, Poelman & Kessler 2016, Vries *et al*. 2017, Howard *et al*. 2018, Rusman *et al*. 2018). These changes may be a simple loss of plant tissue, resulting in resource competition between herbivores, but may also be of chemical origin, through the induction of herbivore-induced plant defences (Kessler & Halitschke 2007, Ohgushi *et al*. 2007, Poelman *et al*. 2008, Poelman & Kessler 2016). Attacks of herbivores can activate induced defences of plants through the jasmonic acid (JA) and salicylic acid (SA) phytohormonal signalling networks (Pieterse *et al*. 2012, Glas *et al*. 2014, Grinberg-Yaari *et al*. 2015), and different herbivore species can induce different defences. Due to cross-talk between these two phytohormonal pathways, induction of defences by one species may have positive, neutral, or negative effects on performance and occurrence of other species (Rodriguez-Soana *et al*. 2010, Mathur *et al*. 2013, Kant *et al*. 2015), resulting in positive, negative or no effects of herbivores on each other's performance (Thaler *et al*. 2002). If *Ac. guerreronis* and *S. concavuscutum* induce different plant defence responses, coconuts with different induced defences may not only influence the occurrence of *At. bondari* larvae but also the co-occurrence of both mites, as was found in this study (Fig. 1).

Furthermore, changes induced by herbivory may be physical, for example, the habitat construction by species of leaf-rolling caterpillars (Lill & Marquis 2004). In our study system, physical changes as a result of herbivore attacks do occur, for example, the damage caused by the mites may increase the size of the opening between the perianth and the nut, allowing access to other herbivores. Thus, the co-occurrence of the three herbivores studied here may well be the consequence of all such changes induced by the mites on the coconuts. Clearly, to disentangle these different mechanisms, studies of the performance of *At. bondari* larvae on nuts that are both naturally or artificially infested with *Ac. guerreronis*, *S. concavuscutum* or not infested, as well as studies on the preference of larvae and oviposition of females for such nuts are needed.

Atheloca bondari larvae were not totally incapable to access the meristematic region of nuts that were not infested by mites (Fig 1). Attacks by other herbivores or natural increases of the perianth opening may also facilitate the access of *At. bondari* larvae to nuts without mites. However, the distribution of *At. bondari* did not differ among coconuts of distinct ages (Fig 3), suggesting that the natural increase of the opening to the meristematic region in older nuts (Howard & Rodriguez 1991, Lima *et al*. 2012) is not sufficient to allow larval infestation. We recommend a study to measure the size of access to the meristematic region in nuts either infested by *Ac. guerreronis* or *S. concavuscutum*, and not infested by mites.

The presence of *At. bondari* larvae in coconuts seems mostly positively related to infestations by *Ac. guerreronis* (Fig. 1; Fig. 2; Fig. 4a,b). In nuts collected from palm trees, *At. bondari* larvae co-occur with *Ac. guerreronis* more frequently than expected at all ages of nuts, whereas the co-occurrence these species was higher than expected only in fallen nuts of ages 2 and 3 (Fig. 4a,b). The lack of significant co-occurrence between *At. bondari* and *Ac. guerreronis* in older fallen fruits may be due to the low number of these nuts found (Fig. 4b,d; Fig. 5f,h). Apparently, older coconuts tend to fall less than the younger ones, in agreement with observations that the nuts typically fall three to eight weeks after the spathe opens (Cock *et al*. 1985, Lever 1969), where younger nuts are more likely to fall after the herbivore attack (Vanderplank 1959, McKinlay 1965, Williams 1974).

Aceria guerreronis is considered the main pest of coconut palm, where the attack of this mite results in copra yield loss (Mathews *et al*. 2004, Navia *et al*. 2013). In some cases, it has been reported that *Ac. guererronis* infestations cause significant premature coconut drop (Nair 2002, Rezende *et al*. 2016). If *Ac. guerreronis* reduces the vigour and germination of coconut seeds, premature drop of nuts infested by the mite may be advantageous for the coconut palm, because it might reduce the risk of infection of the other nuts in the bunch and reduce the investment in nuts of lower quality. However, many nuts infested with *Ac. guerreronis* produce vigorous seedlings (Haq *et al*. 2002, Regi & Mathews 2004, Beevi *et al*. 2006), hence, the question remains whether feeding by *Ac. guerreronis* is also detrimental for the coconut trees, and not just for commercial production of coconuts. Here we show that infestations by *At. bondari* are correlated with fall of coconuts (Fig. 6a,b,c), whereas infestations with *Ac. guerreronis* are less so (Fig. 6a,c). Thus, the presence of *Ac. guerreronis* in nuts can increase production losses not due to herbivory of this mite, but due to the facilitation of nut attack by other herbivores. Clearly, further study is needed into the causes of prematurely fallen coconuts.

The co-occurrence of *At. bondari* and *S. concavuscutum* was exceptionally low in nuts of age 3, 4 and 5 harvested from trees (Fig. 4c), and the proportion of fallen nuts with *At. bondari* and *S. concavuscutum* did not differ from that of nuts collected from the trees (Fig. 6b). It is not clear to us why *At. bondari* and *S. concavuscutum* co-occur less in nuts of intermediate age, but this may be due to the low quality of the nuts of these ages. We emphasize again the importance of studying the performance of *At. bondari* in nuts that are artificially infested with mites.

In nuts from trees, there is a tendency of *Ac. guerreronis* and *S. concavuscutum* to co-occur less frequently as coconut nuts become older (Fig. 5g), and this tendency cannot be explained by the larger number of old fallen nuts infested by both mites (Fig 5h). Measurements of non-infested coconuts show that the opening between the perianth and the nut surface of nuts of age 2 is 20 - 40 µm (Lima *et al*. 2102). The tiny adult females of *Ac. guerreronis* (36-52 µm thick) (Keifer 1965) can colonize these young nuts, however, adult females of *S. concavuscutum* (110-

125 µm wide) (Lofego & Gondim 2006), may have difficulties to enter the microhabitat of non-infested young nuts. Lima *et al*. (2012) show that infestation by *Ac. guerreronis* increases the opening between the perianth and the meristematic region. The co-occurrence of *Ac. guerreronis* and *S. concavuscutum* in younger nuts may thus be due to facilitation of *S. concavuscutum* by *Ac. guerreronis*, and the less frequent co-occurrence in older fruits may be due to competitive exclusion.

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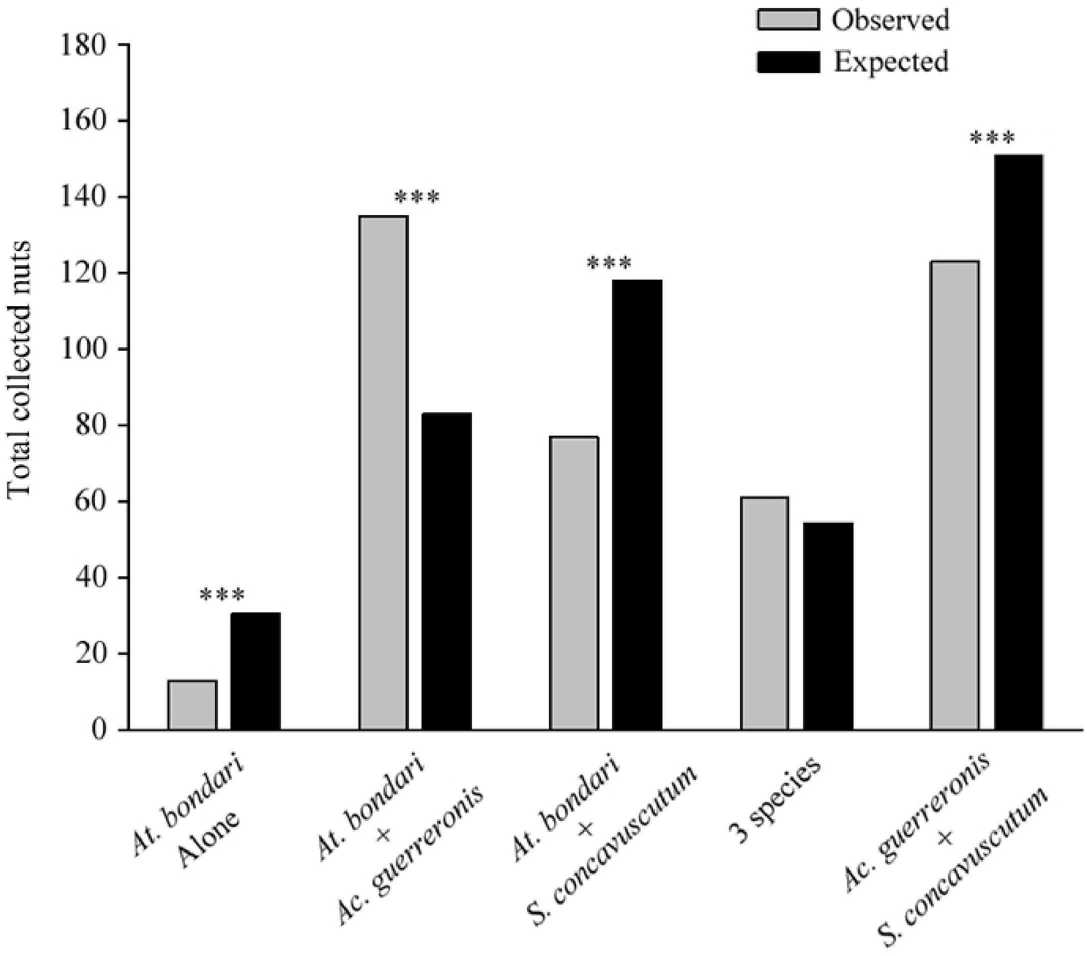


Figure 1. Occurrence of *At. bondari*, *Ac. guerreronis* and *S. concavuscutum* and their co-occurrence in the nuts collected from trees. The grey bars correspond the total number of nuts collected for each category and the black bars represent the number expected. Asterisks indicate significant differences between observed and expected (hypergeometric distribution test, Griffith *et al*. 2016): ***: P < 0.001.

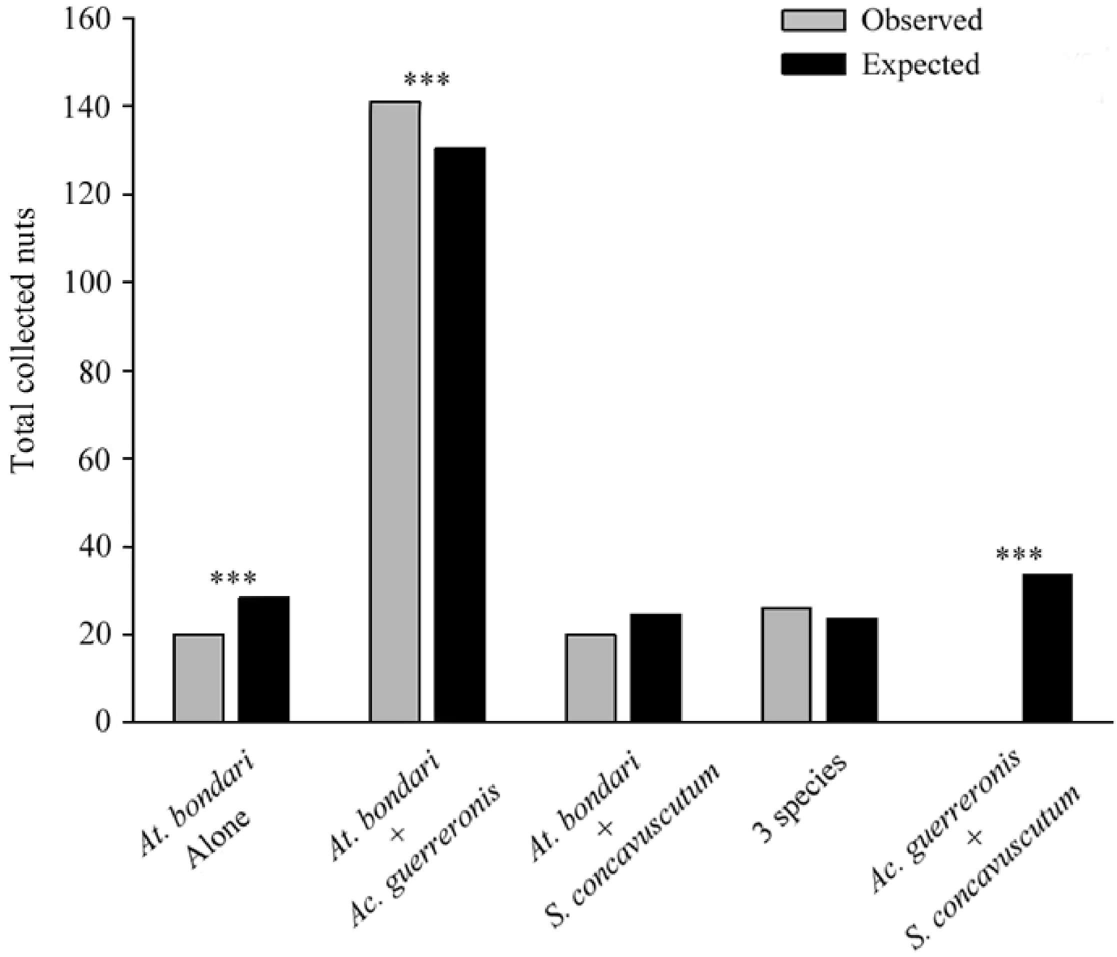


Figure 2. Occurrence of *At. bondari*, *Ac. guerreronis* and *S. concavuscutum* and their co-occurrence in the fallen nuts. The grey bars correspond the total number of nuts collected for each category and the black bars represent the number expected. Asterisks indicate significant differences between observed and expected (hypergeometric distribution test, Griffith *et al.* 2016): ***: $P < 0.001$.

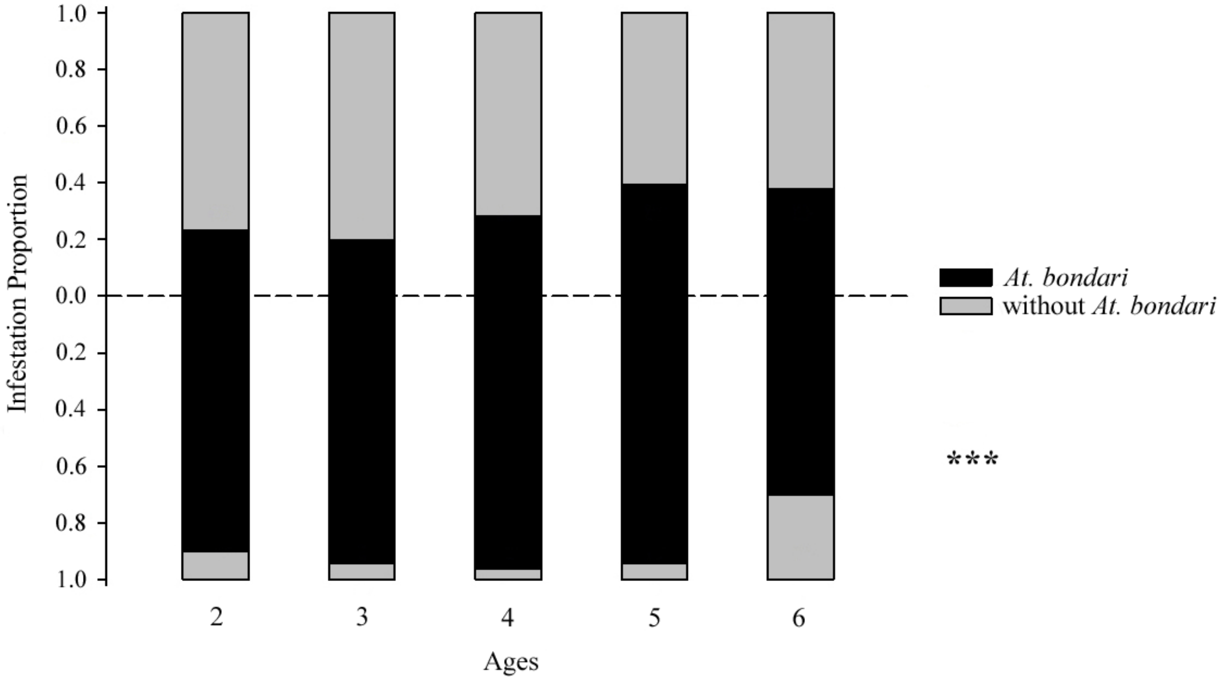


Figure 3. Proportion of *At. bondari* in fallen coconuts and nuts from trees of different ages. Bars below the dashed line represent the proportion of fallen nuts; this above the dashed line represent the proportion of nuts collected from trees. Asterisks indicate significant overall difference between fallen and trees nuts (GLM): ***: P < 0.001.

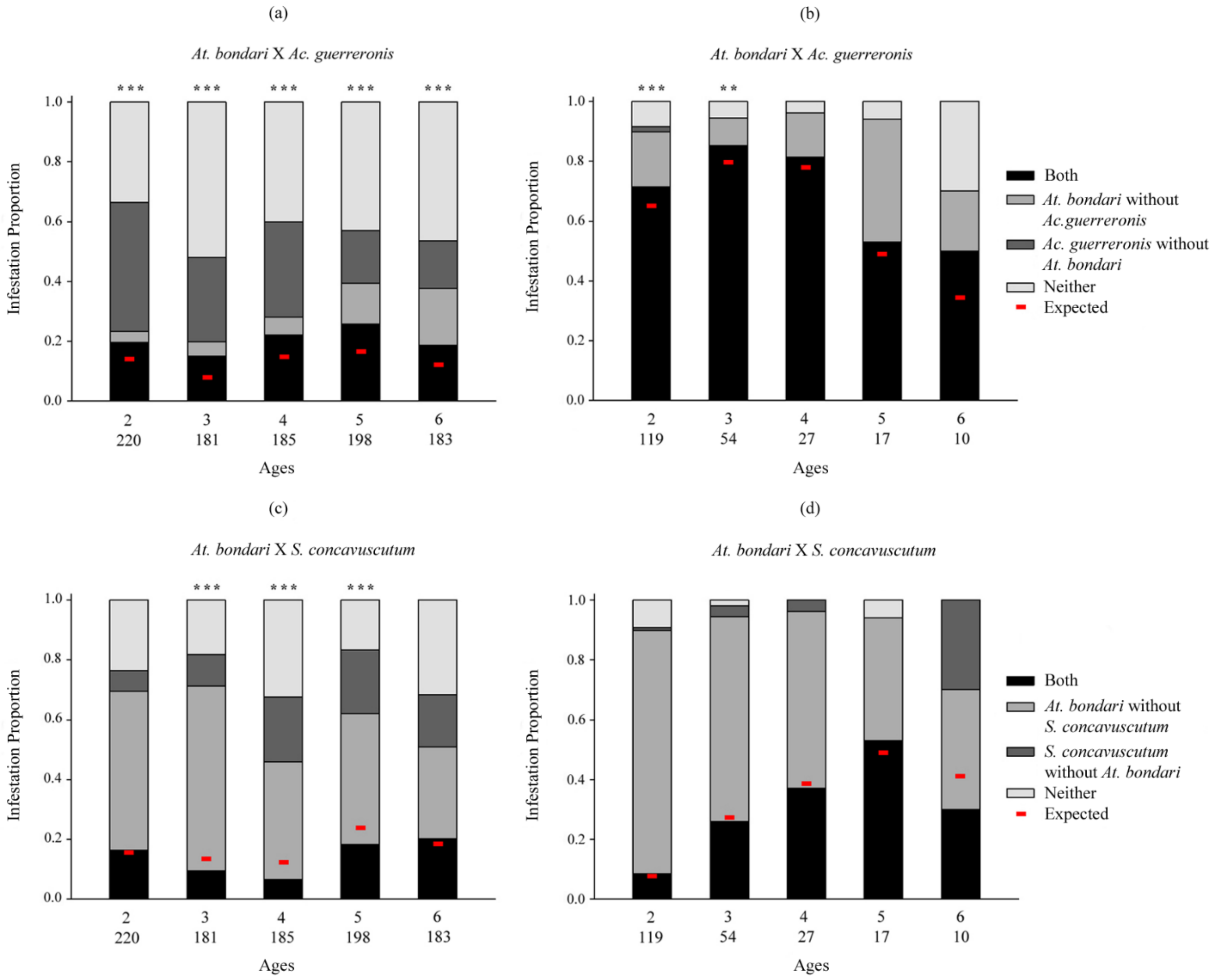
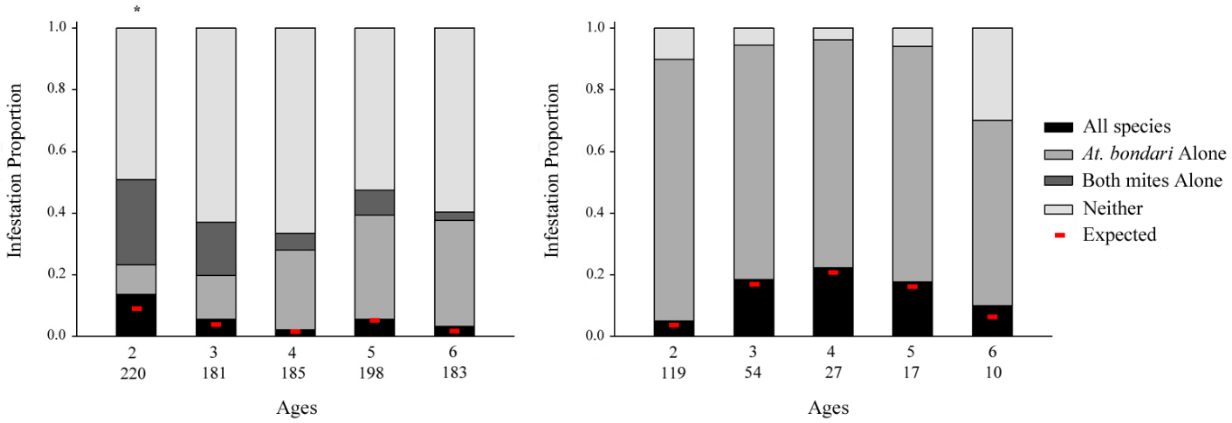
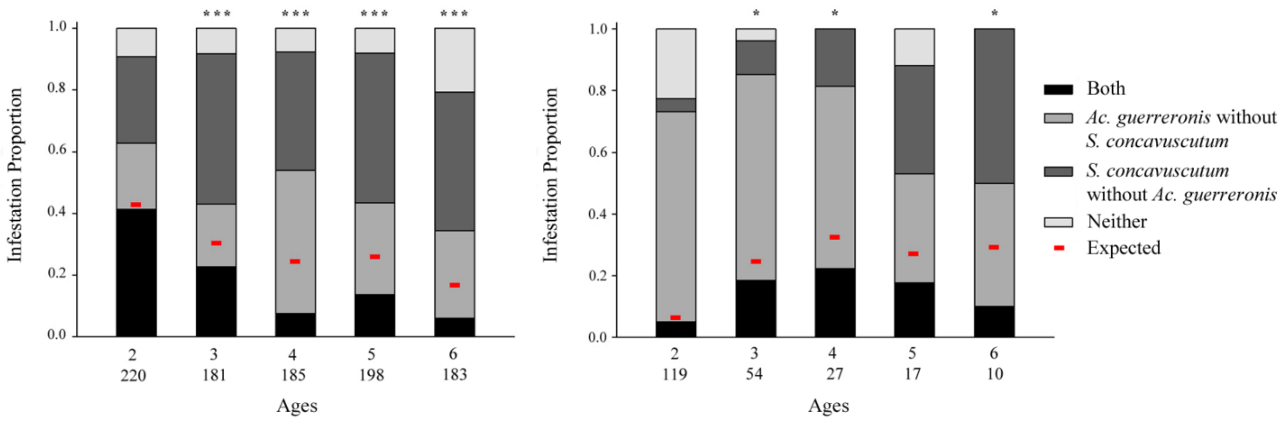


Figure 4. Proportion of *At. bondari*, *Ac. guerreronis* and *S. concavuscutum* and their co-occurrence on coconut fruits of different ages for different combinations of these three species (a – d). Left-hand panels represent the nuts collected from trees; right-hand panels fallen nuts. The red dash indicates the expected proportion of fruits infested by both species. The total numbers of fruits sampled per age are shows below the ages along the horizontal axis. Asterisks indicate significant differences between observed and expected (hypergeometric distribution test, Griffith et al. 2016): **: $P < 0.01$; ***: $P < 0.001$.


(e) All 3 species

(f) All 3 species


(g) *Ac. guerreronis* X *S. concavuscutum*

(h) *Ac. guerreronis* X *S. concavuscutum*

Figure 5. Proportion of *At. bondari*, *Ac. guerreronis* and *S. concavuscutum* and their co-occurrence on coconut fruits of different ages for different combinations of these three species (e – h). Left-hand panels represent the nuts collected from trees; right-hand panels fallen nuts. The red dash indicates the expected proportion of fruits infested by both species. The total numbers of fruits sampled per age are shows below the ages along the horizontal axis. Asterisks indicate significant differences between observed and expected (hypergeometric distribution test, Griffith *et al*. 2016): *: $P < 0.05$; ***: $P < 0.001$.

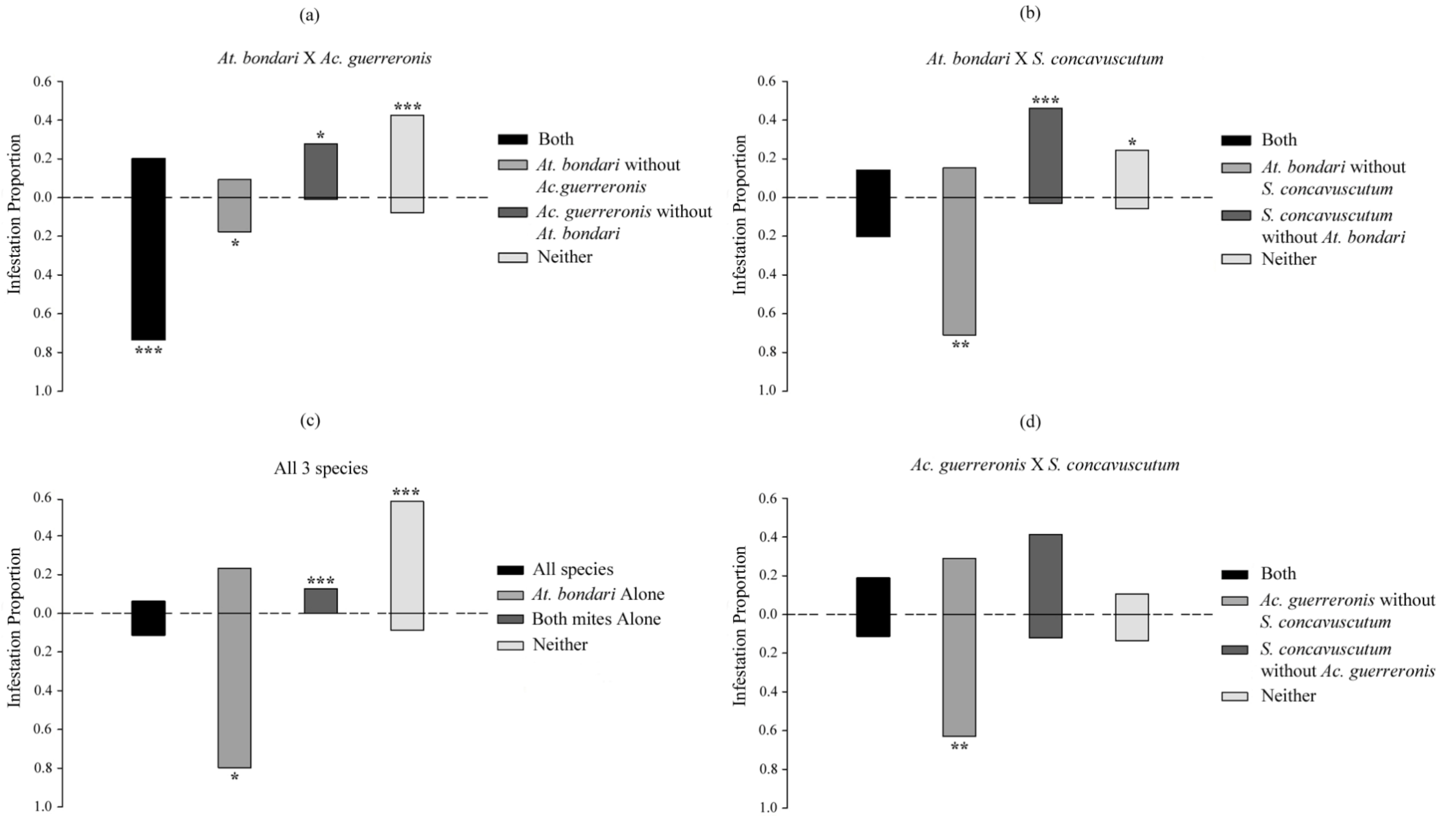


Figure 6. Proportion of *At. bondari*, *Ac. guerreronis* and *S. concavuscutum* and their interactions in fruits collected from tree and fallen fruits. Bars below the dashed line represent the proportion of aborted fruits, above the dashed line the proportion of fruits collected from trees. Asterisks indicate significance with a GLM test: *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$.

CHAPTER 4

DAMAGE OF MITES PROVIDES REFUGE AND AFFECTS THE PREFERENCE AND PERFORMANCE OF SUBSEQUENT HERBIVORE

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ABSTRACT – Damage caused by herbivores often modifies the plant's structure and physiology, which may change the behavior and biology of later-arriving herbivores. Here we studied these associations among the phytophagous mites *Aceria guerreronis* (Acari: Eriophyidae) and *Steneotarsonemus concavuscutum* (Acari: Tarsonemidae) and the moth *Atheloca bondari* (Lepidoptera: Pyralidae). *Aceria guerreronis* is considered the main pest of coconuts, and the other two species play an important economic role only in areas of north-eastern Brazil. These species all develop in the meristematic zone of coconuts. This zone is difficult to access due to the tiny opening between the epicarp and the perianth covering the meristematic zone. Both mites cause necrosis on the epicarp of the nuts, and this necrosis may facilitate access to the meristematic zone for the caterpillars. However, *At. bondari* caterpillars co-occur predominantly with *Ac. gerreronis* and not with S. *concavuscutum*, suggesting that infestation by the caterpillars does not only depend on facilitating the access to the meristem. We therefore evaluated how the caterpillars infest nuts that were either uninfested or infested by *Ac. guerreronis*, *S. concavuscutum*, or by both. We also tested the preference of both larvae and adults, and the performance of *At. bondari* on nuts with these treatments. Caterpillars preferred nuts with easy access to the meristematic region, regardless of the presence of mites. *Atheloca bondari* females showed no preference to oviposit in any of the treatments, but *At. bondari* caterpillars that developed in *Ac. guerreronis*-infested nuts had better performance. *Aceria guerreronis* acts as an ecosystem engineer by providing resource and shelter to *At. bondari*.

KEY WORDS: oviposition choice, larval dispersal, facilitation interaction, mite-insect-plant association

O DANO DE ÁCAROS FORNECE REFÚGIO E AFETA A PREFERÊNCIA E O DESEMPENHO DO HERBIVORO SUBSEQUENTE

RESUMO – Os danos causados pelos herbívoros modificam as estruturas e fisiologia das plantas que podem alterar o comportamento e biologia de herbívoros subsequentes. Esttudou-se as associações entre os ácaros fitófagos *Aceria guerreronis* (Acari: Eriophyidae) e *Steneotarsonemus concavuscutum* (Acari: Tarsonemidae), e a mariposa *Atheloca bondari* (Lepidoptera: Pyralidae). *Aceria guerreronis* é considerado uma das principais pragas do coqueiro, e as outras espécies desempenham uma importância econômica apenas em regiões do nordeste brasileiro. Todas essas espécies se desenvolvem na região meristemática dos frutos de coqueiro. Essa é uma zona de difícil acesso devido a pequena abertura entre o epicarpo e o perianto que cobre a zona meristemática. Ambos os ácaros causam necroses no epicarpo dos frutos, e essas necroses podem facilitar o acesso das lagartas à zona meristemática. Todavia, as lagartas de *At. bondari* coocorrem predominantemente com *Ac. guerreronis* e não com *S. concavuscutum*, sugerindo que a infestação das lagartas não depende apenas da facilidade de acesso ao meristema. Foi avaliado como as lagartas infestam os frutos não infestados, ou infestados apenas por *Ac. guerreronis,* ou por *S. concavuscutum,* ou por ambos os ácaros. Além disso, avaliou-se a preferência tanto das larvas quanto dos adultos, e a performance de *At. bondari* nos frutos com esses diferentes tratamentos. As lagartas preferem frutos com fácil acesso à região meristemática, independente da presença dos ácaros. As fêmeas de *At. bondari* não mostraram preferência em ovipositar em qualquer tratamento, mas as lagartas de *At. bondari* que se desenvolveram em frutos infestados por *Ac. guerreronis* tiveram uma melhor performance. *Aceria guerreronis* atual como um engenheiro do ecossistema por fornecer recurso e abrigo para *At. bondari*.

PALAVRAS-CHAVE: escolha de oviposição, dispersão larval, interação de facilitação, associação ácaro-inseto-planta

Introduction

Herbivore attacks trigger a cascade of metabolic responses in plants, modifying the chemical, physiological, morphological and architectural traits of plants (Karban & Baldwin 1997, Ohgushi 2005, Stam *et al*. 2014, Kant *et al*. 2015). Moreover, herbivory affects the photosynthetic rates and resource allocation from and to storage tissues, which can affect the palatability for herbivores through altered availability of basic nutrients (Karban & Myers 1989, Haukioja 1990, Agrawal 1998, Agrawal *et al*. 1999, Stowe *et al*. 2000, Poveda *et al*. 2012). Thus, the changes in plant traits caused by a herbivore may have negative or positive effects on the rest of the herbivore community on the shared host plant (Karban & Baldwin 1997, Rodriguez-Saona & Thaler 2005, Agrawal *et al*. 2006, Kessler & Halitschke 2007, Ohgushi *et al*. 2007, Ohgushi 2008, Utsumi *et al*. 2009, Hunter *et al*. 2012, Mathur *et al*. 2013, Ali & Agrawal 2014). For example, shelter building by caterpillars results in increased species diversity within a plant (Lill & Marquis 2003), and leaf-rolling caterpillars can improve leaf quality and favour the performance of other herbivores using the leaf roll as shelter (Fukui *et al*. 2002). Moreover, induced plant traits can indicate the presence of potential competitors to subsequent herbivore species (Dicke 2000, Kessler & Baldwin 2001, Stam *et al*. 2018), altering the recruitment to the damaged plant (Pallini *et al*. 1997, Bernasconi *et al*. 1998, Agrawal 1999, Poelman *et al*. 2008, Erb *et al*. 2011, Kroes *et al*. 2016).

Some herbivores are adapted to use specific plant structures that provide not only food but also refuge (Jeffries & Lawton 1984, Berdegue *et al*. 1996, Oppenheim & Gould 2002, Berryman & Hawkins 2006), allowing them to develop in sites with low interspecific competition and high protection from predators and unfavourable climatic factors (Rypstra *et al*. 1999, Langellotto & Denno 2004). Thus, effects of host plants on herbivorous insect fitness measures often varies due to intrinsic differences in nutritional quality, physical and chemical defenses, and risk of attack by natural enemies (Rosenwald *et al*. 2017).

The amount and type of resistance traits change during plant development, therefore herbivore incidence at a particular plant stage will depend on the degree of synchrony between plant phenology and that of herbivores and the natural enemies of those herbivores (Boege & Marquis 2005). However, herbivory can modify the plant defense traits and thus modulate the occurrence of opportunistic herbivores at a particular stage of the plant (Lill & Marquis 2003, Ohgushi 2005, Uesugi et al. 2016). Here, we evaluate how the presence of the mites *Aceria guerreronis* (Acari: Eriophyidae) (Keifer) and *Steneotarsonemus concavuscutum* (Acari: Tarsonemidae) Lofego & Gondin Jr., affects the preference and performance of the moth *Atheloca bondari* (Lepidoptera: Pyralidae) Heinrich. All three species feed on the meristematic zone of coconuts.

In the field, the occurrence of *At. bondari* is positively associated with *Ac. guerreronis*, while the association of *At. bondari* and *S. concavuscutum* is negative (Paz-Neto *et al*. 2020). *Aceria guerreronis* causes necrotic lesions that modify the epicarp of nuts (Aratchige *et al*. 2007, Lima *et al*. 2012), enlarging the opening between the surface of the nut and the perianth. Santana *et al*. (2009) state that *At. bondari* larvae use these lesions to reach the meristematic zone and infest nuts. Thus, *Ac. guerreronis* modulates the availability of resources for *At. bondari*. However, *S. concavuscutum* causes similar necrotic patterns on the epicarp of the nuts (Navia *et al*. 2005, Lofego & Gondim Jr 2006), therefore, necrosis caused by *S. concavuscutum* could also facilitate infestation of nuts by *At. bondari* caterpillars. Because morphological changes caused by herbivory often coincide with plant defense responses (Agrawal 1999, Yoshida *et al*. 2009, Uesugi *et al*. 2016) or nutritional changes (Lou & Baldwin 2004), different qualities of nuts attacked by *Ac. guerreronis* or *S. concavuscutum* may have positive or negative effects on the preference and performance of *At. bondari*. Therefore, the associations among these species are likely to be a result of multiple factors.

Here, we first assessed the size of the opening of the meristematic zone in nuts that were either infested by each mite or not infested. In addition, the infestation ability of the caterpillar, the selection of clean and mite-infested nuts and bunches by both adult females and caterpillars of *At. bondari* and the performance of *At. bondari* on infested and clean nuts was investigated.

Material and Methods

Rearing moths. Nuts that showed signs of the presence of *At. bondari* caterpillars (hole with frass) were collected in Igarassú (Mangue Seco)/PE (7°49' S, 34°50' W) and transported to the laboratory. There, we removed the caterpillars and transferred them to clean nuts collected at the campus of the Federal Rural University of Pernambuco (8º01'S, 34º94'W).

We used the rearing method developed by Santana *et al.* (2011). Three cuts were made in the epidermis of nuts with a scalpel forming a triangular opening (0.5 cm of width and depth) just below the bracts. This procedure was repeated on each of the three sides of the nuts and one caterpillar of *At. bondari* was introduced at each side (i.e. three caterpillars per nut).

The artificially infested nuts were kept in a vertical position using a 10 x 10 cm styrofoam platform with a hole of ~5 cm wide in the middle in which the nut was placed. The platform was placed inside a 12 x 17 cm (diameter and height) plastic container. This container had a hole in the side, covered with a 12 x 8 cm (height and width) mesh (50 µ) to allow ventilation. Three layers of paper towel were placed on the bottom of the container under the platform to collect the moist exudates from the nuts damaged by the caterpillar and to serve as pupation substrate. Because of the rapid decay of the nuts, the caterpillar was transferred to a new nut after 5 days.

The prepupae left the nut to pupate in the towels. These pupae were collected and incubated individually in 2.0 x 3.5 cm (diameter and height) acrylic vials until emergence of the adults. Newly emerged adults were sexed based on the shape of the tip of the abdomen (see Santana *et al*. 2011) and paired in transparent plastic containers as described above. They were fed with a 10 % honey solution placed in a 3 cm (diameter) lid. Females oviposited in grooves on the side of these lids.

The lids with eggs were transferred daily to a new, similar container. Neonate caterpillar (~12 h old) were introduced to nuts using the same method as above. The rearing units were kept at 27 ± 1.5ºC, with a relative humidity of 70 ± 5% and a photoperiod of 12h.

Collection of nuts. For experiments, we collected nuts infested with either *Ac. guerreronis*, *S. concavuscutum* or both from the coast of Igarassú. We discarded nuts that showed evidence of *At. bondari* infestation (*e.g*. hole with frass).

The symptoms caused by the two mite species differ markedly: *Ac. guerreronis* causes triangular yellow chlorosis while *S. concavuscutum* causes longitudinal yellow stains close to the margin of the perianth, which become necrotic with nut growth. We used nuts with an injury level of *Ac. guerreronis* between 16-32 % on the scale proposed by Galvão *et al*. (2008). Because such a scale is not available for *S. concavuscutum*, we standardized the injury level of this species using the same scale. Based on these characteristic damage patterns, bunches corresponding to leaves 14 from the apex, which are 4 months old, were collected from trees and transported to the laboratory.

Colonization of nuts by *Atheloca bondari* caterpillar. We tested whether damage caused by the two mites facilitated the colonization of the meristematic zone under the perianths by *At. bondari* caterpillar in an experiment on colonization of nuts by caterpillars. Disposable plastic cups (200 ml) were filled with 100 ml of gypsum in water and a 6-cm-long nail was inserted with its head into the plaster, with the pointed end of the nail sticking out above the plaster (Silva *et al*. 2017). After the plaster had dried, the disposable plastic cup was removed and the nail was inserted into the floral aperture of the nuts, resulting in the nut standing on a gypsum pedestal. A barrier of entomological glue (ISCA PEGA®, ISCA Ferramentas e Soluções para Manejo de Pragas, Rio Grande do Sul, Brazil) was applied at 5 cm below the distal parts of the perianth to prevent escape of caterpillars. Each nut represented one experimental unit.

Nuts either infested by *Ac. guerreronis, S. concavuscutum* or both (same damage level) and clean nuts were used for this experiment. We performed twenty replicates (nuts) per treatment. The experimental nut was placed in a tray with water and two neonate caterpillars (<12 h age) were released on the external surface of the perianth with a brush (no. 000). Subsequently, we covered the experimental units with a glass dome and the caterpillars were allowed to settle for 96 hours. Subsequently, we carefully removed the perianths with a staple remover and pruning shears to check for the presence of caterpillars in the meristematic zone of the nuts using a stereomicroscope (Zeiss Stemi DV4). At the same time, we verified the infestation of the nuts by mites. Numbers of nuts infested by *At. bondari* caterpillar were compared among treatments with a Generalized Linear Model (GLM) with a binomial error distribution and a-posteriori contrasts among treatments were assessed by aggregating non-significant factor level (Crawley 2013). The statistical analyses were performed with R (R Development Core Team, 2014).

A similar experiment was done but with manipulated openings between the perianth and the epicarp of the nut to test whether the infestation by caterpillars was related to the size of the opening to the meristematic zone. We increased the size of access to the meristematic zone by inserting a 3 cm long and 3 mm thick wooden stick below the perianths and evaluating the colonization of the meristematic tissue by *At. bondari* caterpillars using two different categories of nuts: (i) *S. concavuscutum*-infested nuts with access manipulation and (ii) non-infested nuts with access manipulation. In nuts infested with *S. concavuscutum*, the stick was placed at the offside with necrosis caused by the mites. After inserting the sticks, caterpillars were released, and infested nuts were collected as described above. We performed twenty replicates (nuts) per treatment. *Aceria guerreronis*-infested nuts were not used in this experiment because the previous experiment showed that many caterpillars settled under the perianth of such nuts without enlarged opening.

Caterpillar preference. For this experiment, we collected nuts either infested by *Ac. guerreronis*, by *S. concavuscutum* or not infested (see “Collection of nuts”). We also used nuts of which the openings of the meristematic region were manipulated as above. Fruits infested with mites received the stick at the site of the necrosis caused by the mites.

Caterpillars and *Ac. guerreronis* may have the same preference for certain nuts, irrespective of the presence of this other species, resulting in a positive association between these species without the moths actually preferring nuts infested with these mites. We therefore included a treatment where nuts were artificially infested with *Ac. guerreronis*, thus eliminating the possible preference of the mites for certain types of nuts. To this end, *Ac. guerreronis*-infested nuts were collected on Igarassú (Mangue Seco) and transported to the laboratory. The bracts of these nuts were removed with a staple remover and pruning shears. Mites from these nuts were taken to trees with non-infested nuts on the campus, trees were climbed using a ladder and the mites were transferred to two-month-old nuts with a brush (no. 000). When the nuts reached 4 months of age and an injury level between 16-32 % (see Galvão *et al*. 2008), they were collected and taken to the laboratory. This resulted in nuts with four different treatments: 1. and 2. nuts naturally infested by *Ac. guerreronis* or *S. concavuscutum* respectively; 3. non-infested nuts; 4. artificially infested nuts with *Ac. guerreronis*.

The floral aperture of each nut was pressed onto a nail, fixed in a block of plaster (see Silva *et al*., 2017 and above). Two nuts were aligned with the spikelets pointing towards each other, where they were connected with modelling clay, thus forming a runway for the caterpillars.

Per replicate, one nut of each of two treatments was used. Care was taken that the position of the various treatments differed among replicates to correct for unforeseen asymmetries in the set-up or the environment. The distance between the nuts was 20 cm (10 cm per spikelet). To prevent caterpillars escaping from the nuts, each nut received a barrier of entomological glue as above.

We used twenty replicates per treatment, where each replicate received eight neonate caterpillars (<12 h age) of *At. bondari*. The caterpillars were placed on the modelling clay with a brush (no. 000). The experimental units were covered with a glass dome to minimize influence of laboratory odour, and the caterpillars could crawl for 24 hours.

We checked the nuts as explained in the section "Colonization of nuts by *Atheloca bondari* caterpillar". The number of nuts infested by *At. bondari* caterpillar was assessed and the preference was analysed using a Binomial test (P = 0.5) (Siegel and Castellan 1988).

Measurement of the opening to the meristematic zone of nuts and the cephalic capsule of caterpillar. We collected twenty nuts according to the criteria described in the section "Collection of nuts". Because cutting off the perianth may increase the natural size of the access to the meristematic region, we used a method used by Aratchige *et al*. (2007) and Lima *et al*. (2012). A scalpel was used to cut the mesocarp around the nuts just below the lower extremity of the perianth, thus we took out the top of the nuts and the perianth was left intact. The underside of the perianth of the nuts was photographed under a dissecting microscope (at 40×), using the software Fly capture (v. 1.7, Point Grey Research). Subsequently, the distance between the edge of the bract and the subjacent surface of the fruit was measured using the software Image Plus (v. 2.0, Motic China Group, Xiamen, China). As the level of necrotic lesion caused by mites differs among the sides of the nuts, we always photographed the side with the biggest necrotic lesion. Whenever the necrotic lesion was cracked, we measured the distance from the bottom of the slit to the edge of the bract.

To measure the cephalic capsule, we killed twenty neonate caterpillars (<12h age) by freezing, and subsequently photographed their cephalic capsule and measured its height using a dissecting microscope and the software described above.

The variation of the size of the access to the meristematic zone of nuts infested by different mites and non-infested nuts was compared with the cephalic capsule of *At. bondari* caterpillar using a Generalized Linear Model (GLM). Contrasts were assessed with the Tukey method.

Oviposition. We performed a test to evaluate whether mated females oviposited more in coconut bunches with mites than in non-infested bunches. The mites-infested bunches of four months old were collected as described above. We selected 10 nuts and extracted the remaining nuts from the bunch. The spikelets of the selected nuts were cut to a length of 20 cm.

Oviposition of *At. bondari* was assessed in a cage (120 x 100 x 100 cm) constructed from PVC pipes and covered with mesh (50 µ). The cage was positioned in a greenhouse on the campus, Hobo Data Loggers® were used to record temperature and relative humidity inside the greenhouse for the duration of the experiment. Inside the cage, the bunches were kept vertically using a 10-liter bucket full of plaster. A hole 10 cm x 15 cm (diameter and height) in the middle of the plaster served to secure the base of the bunches. To feed adults we provided 10 lids (5 cm diameter) filled with a 10% honey solution on the floor of the cage. Four mated females of *At. bondari* were released into the cage and could oviposit for two days in a bunch of each treatment following three experimental designs: (i) *Ac. guerreronis*-infested bunches; (ii) *S. concavuscutum*-infested bunches; (iii) non-infested bunches. The test was replicated five times. The numbers of eggs on the bunches were compared with a Generalized Linear Model (GLM) using a quasi Poisson error distribution. In addition, the numbers of eggs deposited on different parts of the bunches of the different treatments were analysed with a GLM with a Binomial error distribution.

We also performed an oviposition preference test. In this test, females were allowed to oviposit on two bunches of the following combinations: (i) *Ac. guerreronis*-infested bunches *vs*. *S. concavuscutum*-infested bunches; (ii) *Ac. guerreronis*-infested bunches *vs*. non-infested bunches; (iii) *S. concavuscutum*-infested bunches *vs*. non-infested bunches. At the end of the test, the bunches were taken to the laboratory and moth eggs were counted using a stereomicroscope (Zeiss Stemi DV4). The numbers of eggs on the paired bunches were also analysed with a GLM with a Poisson error distribution. Contrasts were assessed with the Tukey method.

Caterpillar development. We carried out an experiment to observe if the development of *At. bondari* caterpillar was affected by the presence of the mites in the nuts. We evaluated the survival of caterpillars until pupa, length and survival of the caterpillar-adult period, and pupal weight using the following treatments: (i) *Ac. guerreronis*-infested nuts; (ii) *S. concavuscutum*-infested nuts; (iii) non-infested nuts.

Coconut trees were climbed using a ladder and bunches that were either infested by *Ac. guerreronis*, by *S. concavuscutum* or were not infested were selected using the criteria as outlined above. A 3-cm-long wood stick (3 mm thick) was inserted below the perianth of the nuts to increase the access of caterpillars to the meristematic region. Nuts infested with mites received the stick at the site of the necrosis caused by the mites. We released one neonate caterpillar (<12 hours old) of *At. bondari* into the access created by the insertion of the stick. The artificially *At. bondari*-infested nuts were covered with a mesh (50 µ) tied with string to reduce escapes of the caterpillar and further infestations.

To forestall fall of nuts caused by phytophagous feeding (see Paz-Neto *et al*. 2020), all nuts were removed nine days after infestation with the caterpillars and transported carefully to the laboratory. The nuts were kept in plastic containers as described above (“Rearing moths”). We observed the nuts daily until the beginning of pupation. Completely formed, brown pupae were collected, weighed and incubated individually in 2.0 x 3.5 cm (diameter and height) acrylic vials until emergence of the adults. The caterpillars were considered unviable when they started to feed but did not develop into pupae. We discarded replicates in which the nuts showed no sign of caterpillar feeding.

The proportion of individuals becoming pupae and pupal weight data were analysed with Generalized Linear Model (GLM) using a binomial error distribution and a Gaussian error distribution respectively. Developmental rates of surviving individuals were compared among treatments with a Cox proportional hazards model using the log-rank test.

Results

Colonization of nuts by *Atheloca bondari* caterpillars. The infestation of nuts by different species of mites affected the colonization of *At. bondari* caterpillars (Fig. 1A, GLM: $\text{Chi}^2 = 45.8$, d.f. = 3, $P < 0.001$). *Atheloca bondari* caterpillars were not found in the meristematic region of nuts not infested by mites. The colonization proportion of *At. bondari* caterpillars in *Ac. guerreronis*-infested nuts was higher than nuts infested by *S. concavuscutum* or by both mites (Fig. 1A), while the colonization proportion of *At. bondari* caterpillars did not differ between *S. concavuscutum* and nuts infested by both mites (Fig. 1A).

When the access to the meristematic zone was manipulated, there a larger proportion of nuts colonized by caterpillars, and there was no significant difference between uninfested nuts and nuts infested with *S. concavuscutum* (Fig. 1B, GLM: $\text{Chi}^2 = 0.41$, d.f. = 1, $P = 0.52$).

Caterpilllar preference. In tests without manipulation of access to the meristematic zone, the proportion of nuts colonized by *At. bondari* caterpillars was significantly higher when nuts were infested with *Ac. guerreronis*, either naturally (Fig. 2A, binomial test: $P < 0.001$) or artificially infested (Fig. 2A, binomial test: $P < 0.001$), than of nuts without mites. In contrast, caterpillars that could choose between *Ac. guerreronis*-infested and *S. concavuscutum*-infested nuts did not show a significant preference (Fig. 2A, binomial test: $P = 0.194$). Furthermore, not one caterpillar was found below the perianth when offered *S. concavuscutum*-infested and non-infested nuts (Fig. 2A).

When we manipulated the access to the meristematic zone of the coconuts, the caterpillars did not show a preference in any of the combinations tested (Fig. 2B) (*Ac. guerreronis*-infested nuts *vs* *S. concavuscutum*-infested nuts, $P = 0.5$; *Ac. guerreronis*-infested nuts *vs* non-infested nuts, $P = 0.108$; *S. concavuscutum*-infested nuts *vs* non-infested nuts, $P = 0.05$).

When we tested nuts with manipulation of the entrance of the meristematic zone against un-manipulated nuts, *At. bondari* caterpillars preferred the nuts with the opening manipulation (Fig. 2C), except for the combination of *Ac. guerreronis*-infested nuts and non-infested, manipulated nuts, where no preference was observed (Fig. 2C, $P = 0.151$).

Measurement size of the access to the meristematic zone of nuts and cephalic capsule of caterpillars. The opening of the meristematic region of non-infested nuts and nuts infested by mites and the cephalic capsule size of the caterpillars differed significantly (Fig. 3, GLM, $F_{3,76}$, $P < 0.001$). The cephalic capsule size of neonate *At. bondari* caterpillars was significantly smaller than the opening to the meristematic zone of *Ac. guerreronis*-infested nuts), significantly larger than the opening of non-infested nuts, and did not differ significantly from the opening of *S. concavuscutum*-infested nuts (Fig. 3).

Oviposition. In the no-choice test, the average number of *At. bondari* eggs in the different treatments was significantly different (Fig. 4, GLM: $F_{2,12} = 4.10$, $P = 0.044$), and females laid more eggs in bunches infested by *S. concavuscutum* than bunches not infested by mites. The distribution of eggs over the different parts of the bunches did not differ significantly among treatment (Fig. 4, GLM: $F_{2,12} = 2.63$, $P = 0.11$).

When offered a choice, females of *At. bondari* did not show a clear consistent preference: the variation among replicates was significant for all three combinations of coconut treatment (Fig. 5, GLM: interaction between treatment and replicate, all $P < 0.001$).

Caterpillar development. A larger proportion of *Atheloca bondari* caterpillars that grew on nuts infested by *Ac. guererronis* developed into pupa than in other treatments (Fig. 6A, GLM: $Chi^2 = 7.93$, d.f. = 2, $P = 0.019$). Furthermore, *At. bondari* caterpillars that developed on nuts previously infested by *Ac. guerreronis* or non-infested nuts formed heavier pupae than caterpillars that developed on nuts infested by *S. concavuscutum* (Fig. 6B. GLM: $F_{2,55} = 8.17$, $P < 0.001$). Developmental periods of caterpillars into pupae differed significantly among treatments (Fig. 6C, log-rank statistic: 8.45, d.f. = 2 $P= 0.015$). *Atheloca bondari* caterpillars that grew on nuts infested by *Ac. guerreronis* developed faster into pupa than those on uninfested nuts, while there was no significant difference between caterpillars that developed on nuts infested by *S. concavuscutum* and the other treatments.

Discussion

Taken together, our results suggest that *At. bondari* is an opportunistic herbivore that benefits from infestations of coconuts by mites, which can result in increases of the opening between the epicarp and the perianth, thus facilitating access to highly nutritious tissues under the perianth. Our conclusion is based on several observations. First, caterpillars did not colonize nuts that were not infested by mites or colonized a low proportion of nuts that were infested by *S. concavuscutum*. Second, when the openings were experimentally enlarged, the caterpillars did infest nuts with larger openings, irrespective of the presence of mites, suggesting that it is mainly the opening, and not the presence of mites, that determines infestation by the caterpillars. Third, measurements of the openings and comparing them to the height of the cephalic capsule of the caterpillars shows that indeed only the openings of nuts infested with *Ac. guerreronis* are large enough to allow entrance of the caterpillars. Although *Ac. guerreronis* and *S. concavuscutum* cause similar injury patterns (Navia *et al*. 2005, Lofego & Gondim Jr 2006), our detailed analysis revealed minute differences between the necroses caused by these two mites. The necrosis caused by *Ac. guerreronis* often cause deep slits in the epicarp (Fig. 7), whereas necrosis by *S. concavuscutum* does not cause this, and the resulting openings of the latter are only sometimes large enough to allow access by the caterpillars.

Nuts that were infested by both mites showed a low percentage of infestation of *At. bondari* caterpillars. In these nuts, the necrosis caused by the two mites often overlap, and the necrosis caused by *S. concavuscutum* may modify the physical pattern of necrosis caused by *Ac. guerreronis*. Thus*,* while necrosis caused by *Ac. guerreronis* facilitates *At. bondari* caterpillars to reach and grow in the meristematic zone of coconuts (Santana *et al*. 2009), *S. concavuscutum* may impede the infestation of nuts by *At. bondari* caterpillars.

The infestation of *Ac. guerreronis* not only facilitated access to the meristematic zone of the nuts, but also *At. bondari* caterpillars performed better in nuts infested by this mite than in *S. concavuscutum*-infested or non-infested nuts. The feeding of *At. bondari* caterpillars favors the growth of pathogens in the meristematic zone of the nuts, but nuts infested by *Ac. guerrenonis* take longer to rot (Fig. 8). The herbivory can facilitate the infection of plant tissue by pathogens (Daleo *et al*. 2009), in the other hand, attack by herbivores also can activate plant induced-defences that then reduce pathogen infection (Hatcher & Paul 2000, Paul *et al*. 2000, Hatcher *et al*. 2004, Taylor *et al*. 2004). For example, the eriophyid mites, *Aculops lycopersici* induce in tomato SA-defenses that inhibited the growth of the bacteria *Pseudomonas syringae* (Glas *et al*. 2014) while *Schizoempodium mesophyllincola* suppresses the growth of *Melampsora* rust fungi since mite-damaged mesophyll will not support rust (Busby et al. 2019). Infection by pathogens can affect the nutritional quality and defense metabolites of plant (Hatcher 1995, Lazebnik *et al*. 2014, Rosa *et al*. 2018) and consequently affect the development and host selection behaviour of herbivores (Rostás & Hilker 2002, Shikano *et al*. 2017, Rosa *et al*. 2018). In this way, *At. bondari* may have a worse performance in nuts not infested by *Ac. guerreronis* as a result of *Ac. guerreronis*-coconuts-pathogen interaction, but we emphasize that this issue needs to be further explored.

We observed that some coconuts fell 9 days after the colonization of the *At. bondari* caterpillars, despite this, the caterpillars completed the development in the nuts removed from the palm tree. Thus, the collection and disposal of fallen coconuts can be an important strategy to control *At. bondari*. Plants can induce the abscission of both vegetative and reproductive parts to defend against pathogens (Patharkar *et al*. 2017, Patharkar & Walker 2019). The attack of *At. bondari* caterpillar increases the proportion of fallen nuts (Paz-Neto *et al*. 2020). *Aceria guerreronis* is considered the main cause for abortion of coconut (Doreste 1968, Wickramananda *et al*. 2007, Rezende *et al*. 2016), but these studies do not consider the interaction with other organisms. For example, Lakshmanan & Jagadeesan (2004) showed that the secondary infection of the fungus *Botryodiplodia theobromae* caused a higher fall of nuts than the only infestation by *Ac. guerreronis*. This result makes sense, since a large number of *Ac. guerreronis*-infested nuts reach maturation. Due to the low active dispersion ability of both *Ac. guerreronis* (Galvão *et al*. 2012) and *S. concavuscutum* (França *et al*. 2018), this mites on fallen nuts have little chance to survive. Thus, the attack of *At. bondari* caterpillar on nuts seems to be disadvantageous to the mites.

Atheloca bondari females did not showed preference to oviposit on bunches infested by *Ac. guerreronis*, where eggs were laid randomly between the bunches either infested by *Ac. guerreronis*, *S. concavuscutum* or not infested. Furthermore, a large number of *At. bondari* eggs were found on spikelets and spines, thus, after hatching, the caterpillars have to move within a bunch to find a nut to infest, thereby the behaviour of the caterpillars has a key role in the selection of nuts. However, the *At. bondari* caterpillars also showed no preference to *Ac. guerreronis*-infested nuts. Caterpillars may choose worse quality food in exchange for better protection (Denno *et al*. 1990, Singer *et al*. 2004a, Singer *et al*. 2004b). The coconuts offers both food and shelter for *At. bondari* caterpillars. Thus, *At. bondari* caterpillar can prioritize finding a safe place if the protection against natural enemies or environmental conditions overcomes the disadvantage of developing in worse quality nuts. Besides nuts *At. bondari* caterpillars can develop by feeding on male and female flowers of *C. nucifera* (Cock & Burris 2013). Unlike what happens in the nuts, the *At. bondari* caterpillars pierce the exocarp of the flowers (Bondar 1940). Since the caterpillars do not need the mites to feed on the flowers, the *Ac. guerreronis* infestation should not play a limiting factor to *At. bondari* survival, thus population of *At. bondari* may not be selected to differentiate bunhes or nuts infested by *Ac. guerreronis*. But as flowers are much smaller than coconuts, caterpillars may need to crawl to feed on various flowers to complete their development. How the greater energy expenditure can affect fitness, the association with *Ac. guerreronis* can provides adaptive advantage to *At. bondari*. However, there are no studies evaluating the biological parameters of *At. bondari* when the larvae feed on the flowers.

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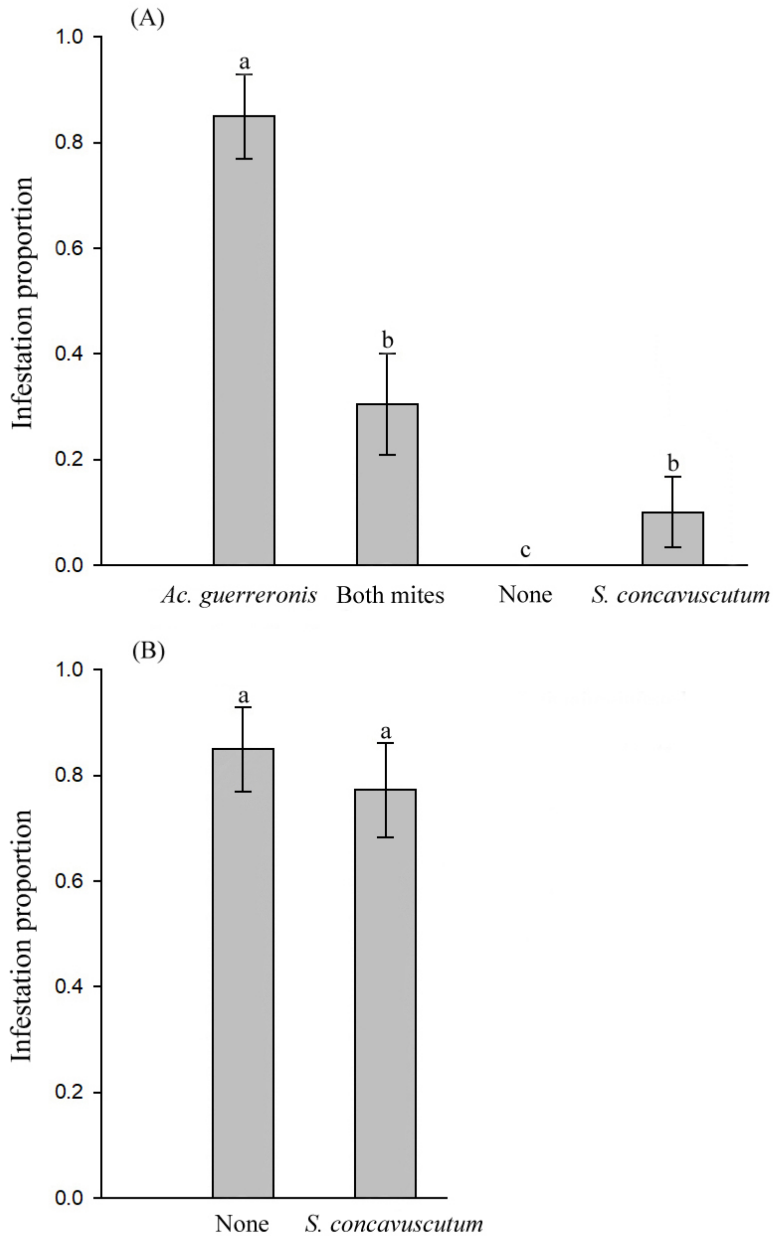
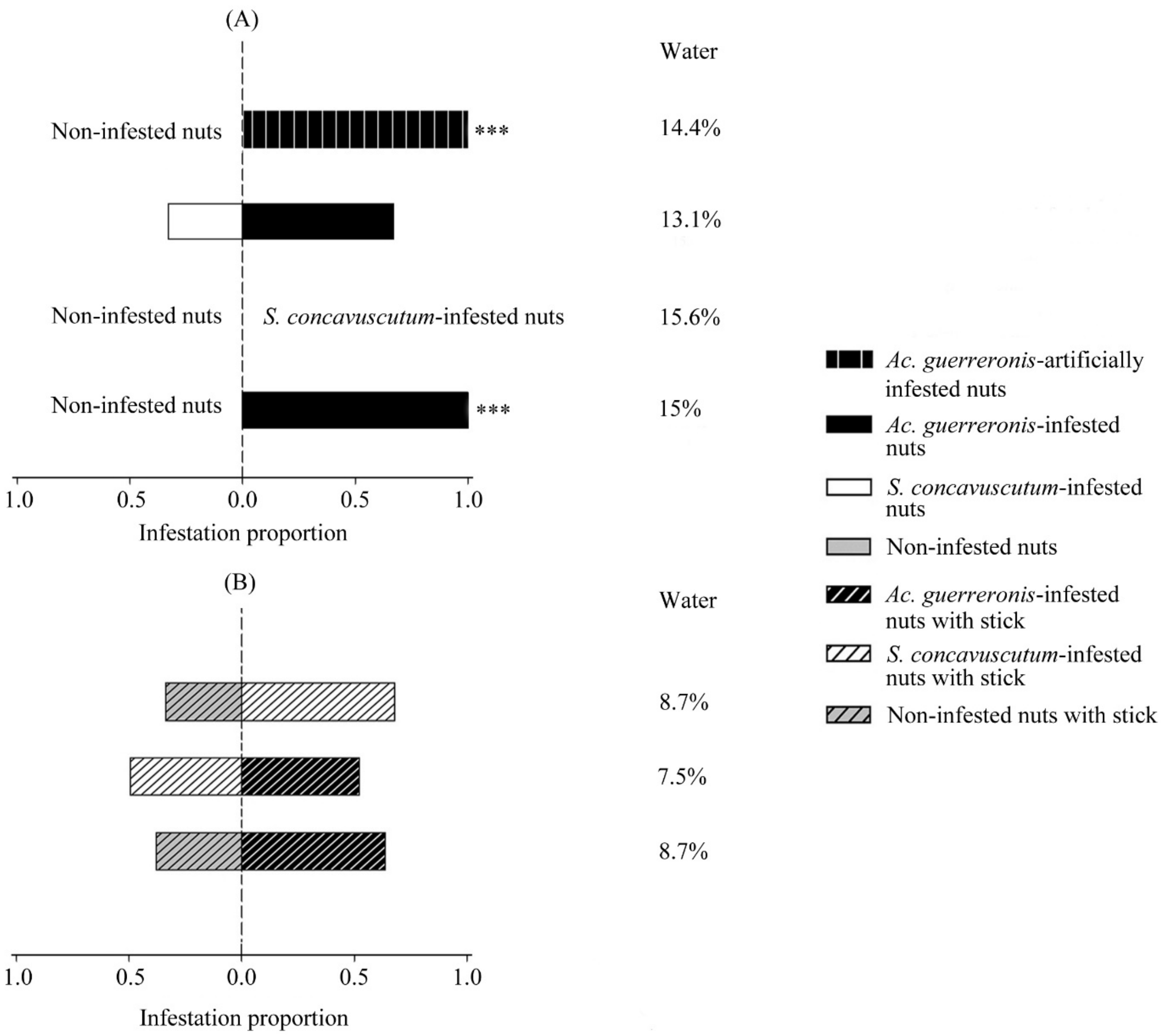


Figure 1. Proportions of nuts either infested by *Ac. guerreronis, S. concavuscutum* or both mites, and non-infested nuts colonized by *At. bondari* caterpillar. Nuts were considered as colonized when the caterpillar were found feeding on the meristematic zone under the perianth. (**A**) nuts without manipulating the access to meristematic zone. (**B**) nuts with manipulating the access to meristematic zone. Small letters indicate significance among different treatments (contrasts after GLM: $P < 0.05$).


(A)
Water
Non-infested nuts
***
14.4%
13.1%
Non-infested nuts
S. concavuscutum-infested nuts
15.6%
Non-infested nuts
***
15%
1.0
0.5
0.0
0.5
1.0
Infestation proportion
(B)
Water
8.7%
7.5%
8.7%
1.0
0.5
0.0
0.5
1.0
Infestation proportion
Ac. guerreronis-artificially infested nuts
Ac. guerreronis-infested nuts
S. concavuscutum-infested nuts
Non-infested nuts
Ac. guerreronis-infested nuts with stick
S. concavuscutum-infested nuts with stick
Non-infested nuts with stick

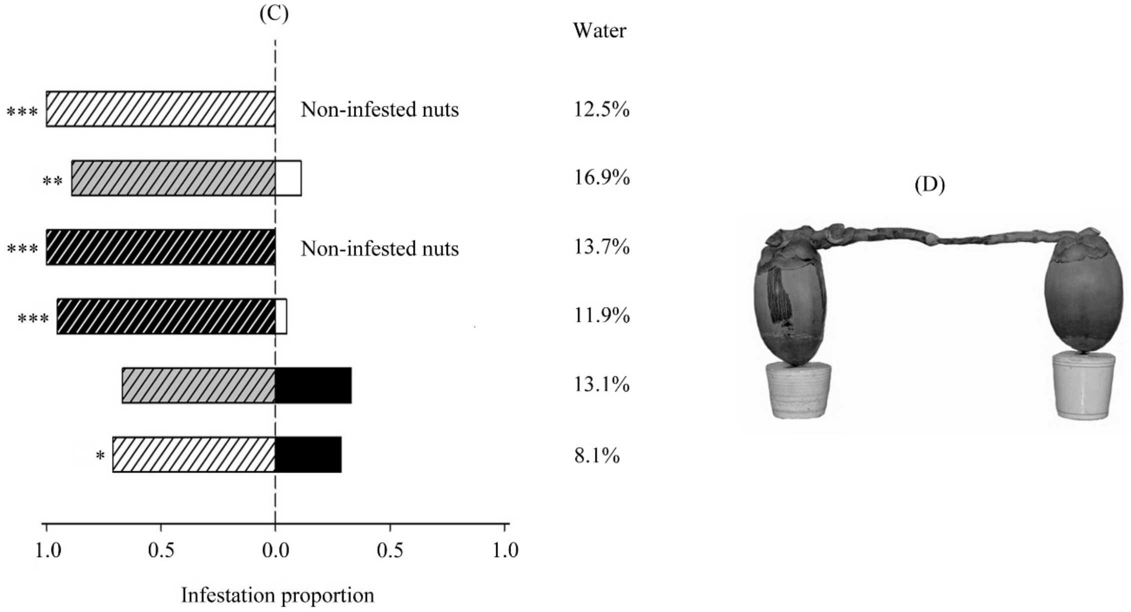


Figure 2. Proportion of nuts colonized by *At. bondari* caterpillar on nuts either *Ac. guerreronis*, *S. concavuscutum*, non-infested or *Ac. guerreronis*-infested artificially. **(A)** nuts without manipulation to meristematic zone. **(B)** nuts with both side of choice with access manipulated. **(C)** nuts with only one side of choice with access manipulated. **(D)** experimental unit photo. **Water:** percentage of caterpillars dropped into the water. Colonization was characterized by the caterpillar feeding on the meristematic zone. Asterisks indicate significance by Binomial test: *: P <0.05; **: P <0.01; ***: P <0.001. Continues on the next page.

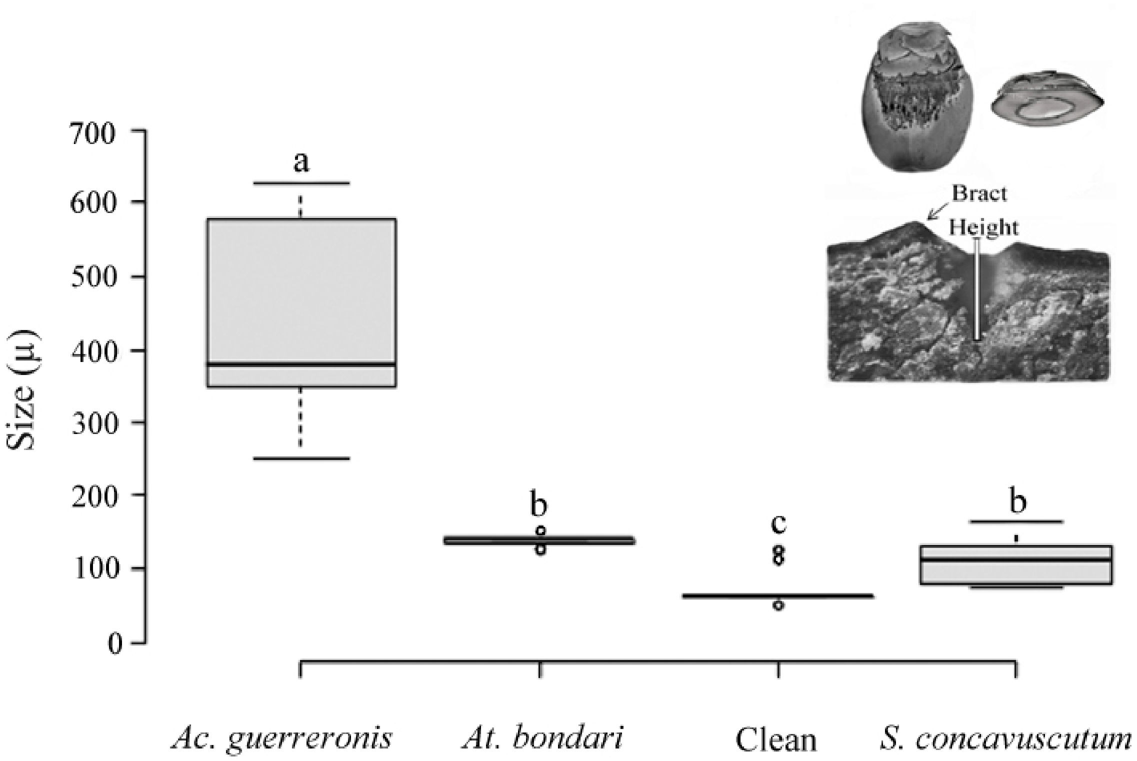


Figure 3. Comparison between the height of the cephalic capsule of the *At. bondari* caterpillar and the space between the perianth and epicarp of nuts either infested by *Ac. guerreronis*, *S. concavuscutum* or non-infested. Small letters indicate significance among different treatments (contrasts after GLM: $P < 0.05$).

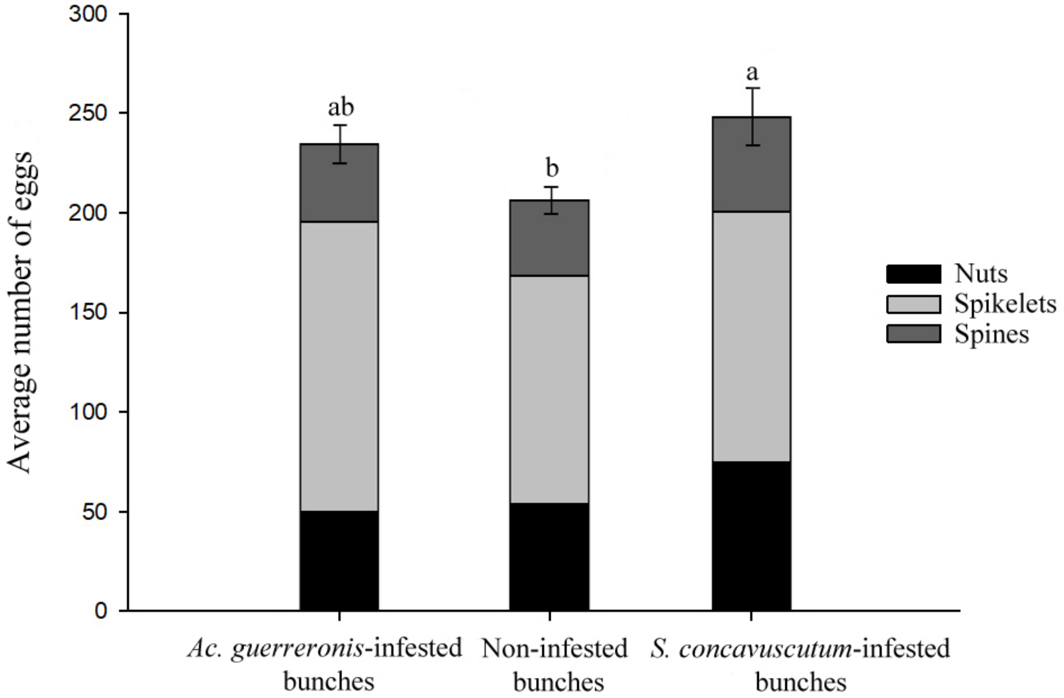


Figure 4. Average number of *At. bondari* eggs in bunches infested by either *Ac. guerreronis*, *S. concavuscutum* or not infested. Different colours in the bars show where the eggs were found. Small letters indicate significance by GLM test: $P < 0.05$.

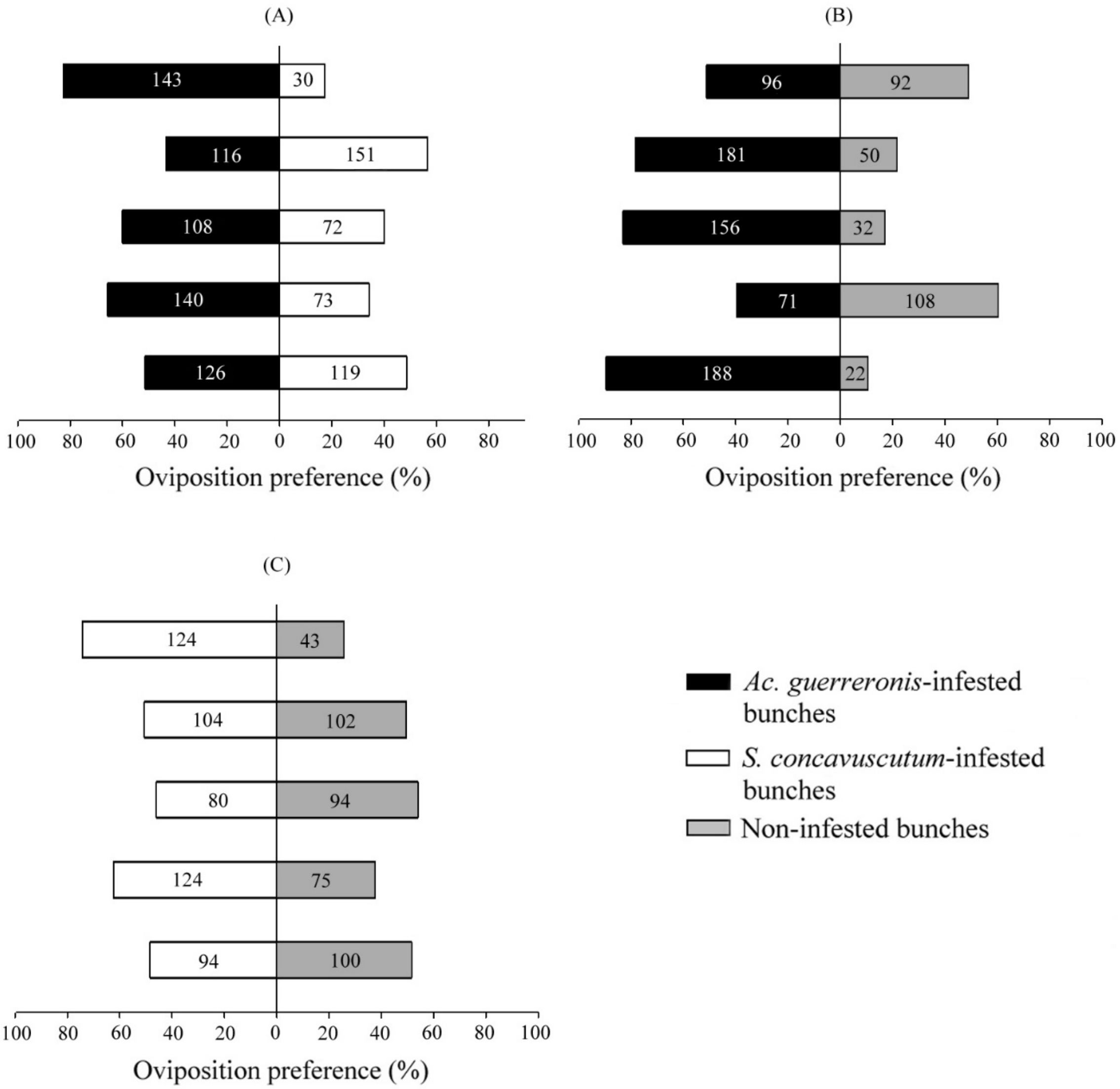
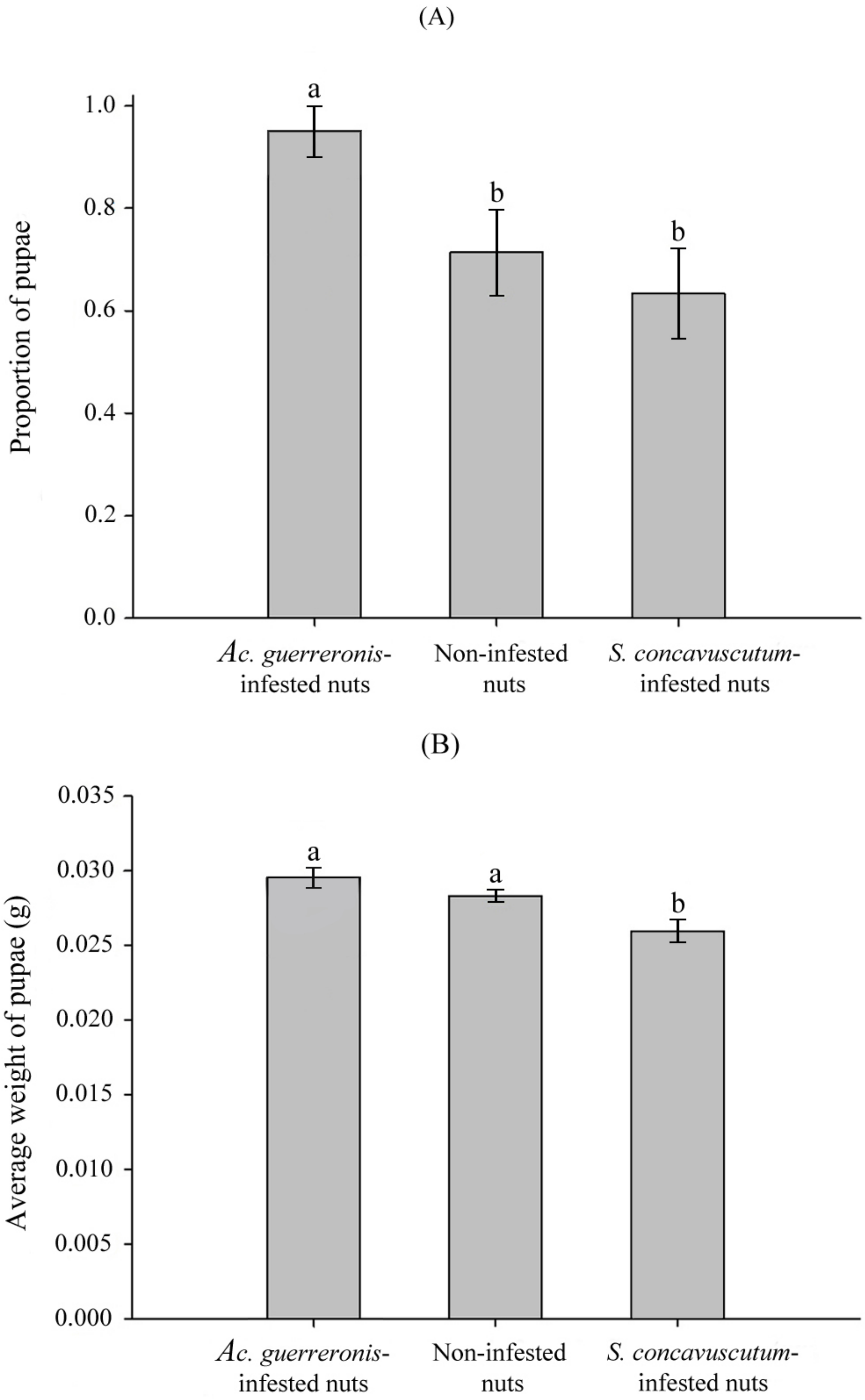


Figure 5. Oviposition preference of *At. bondari* to bunches infested either by *Ac. guerreronis*, *S. concavuscutum* and non-infested. **(A)** contracts between *Ac. guerreronis*-infested and *S. concavuscutum*-infested bunches. **(B)** contracts between *Ac. guerreronis*-infested and non-infested bunches. **(C)** contracts between *S. concavuscutum*-infested and non-infested bunches. The bars represent the percentage of *At. bondari* eggs in each replicate. Numbers inside the bars indicate the amount of *At. bondari* eggs.


(A)
Proportion of pupae
1.0
0.8
0.6
0.4
0.2
0.0
a
b
b
Ac. guerreronis-infested nuts
Non-infested nuts
S. concavuscutum-infested nuts
(B)
Average weight of pupae (g)
0.035
0.030
0.025
0.020
0.015
0.010
0.005
0.000
a
a
b
Ac. guerreronis-infested nuts
Non-infested nuts
S. concavuscutum-infested nuts

(C)

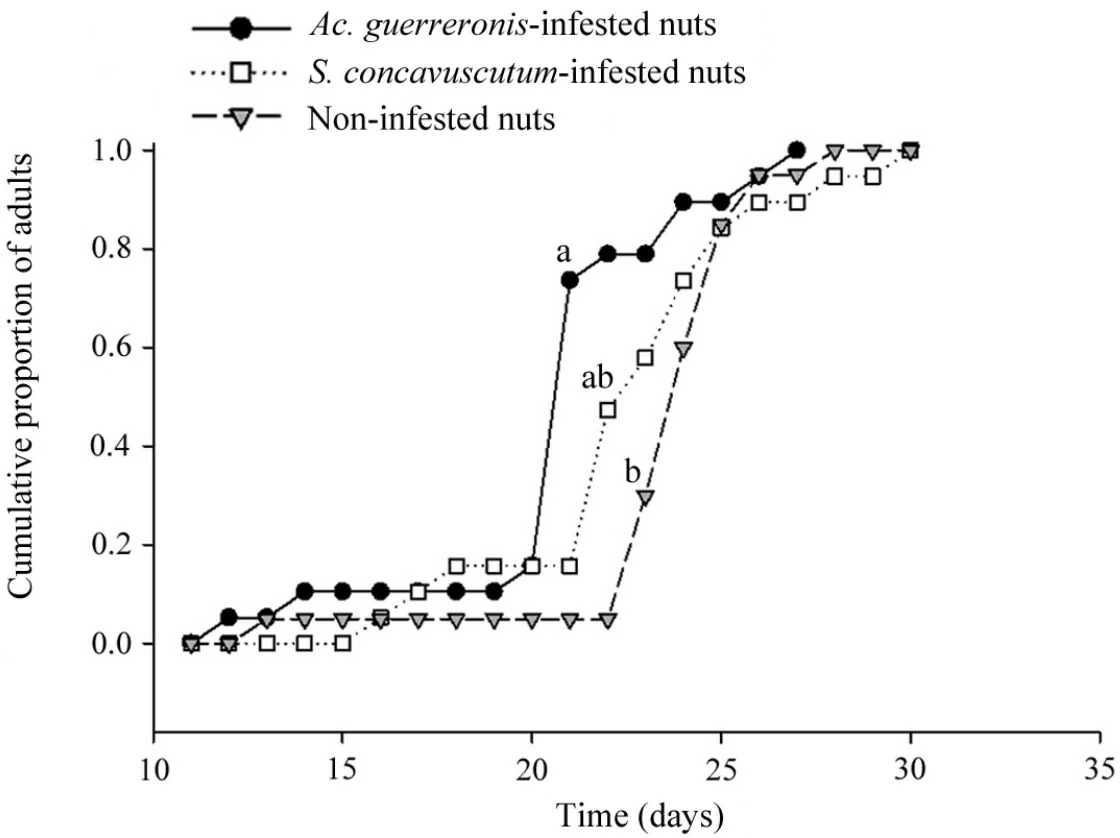


Figure 6. *Atheloca bondari* performance in infested nuts either by *Ac. guerreronis*, *S. concavuscutum* and non-infested. **(A)** proportion of *At. bondari* caterpillar reaching pupa. **(B)** average weight of pupae. **(C)** *At. bondari* caterpillar-adult survival. Small letters indicated significance by GLM test: P <0.05.

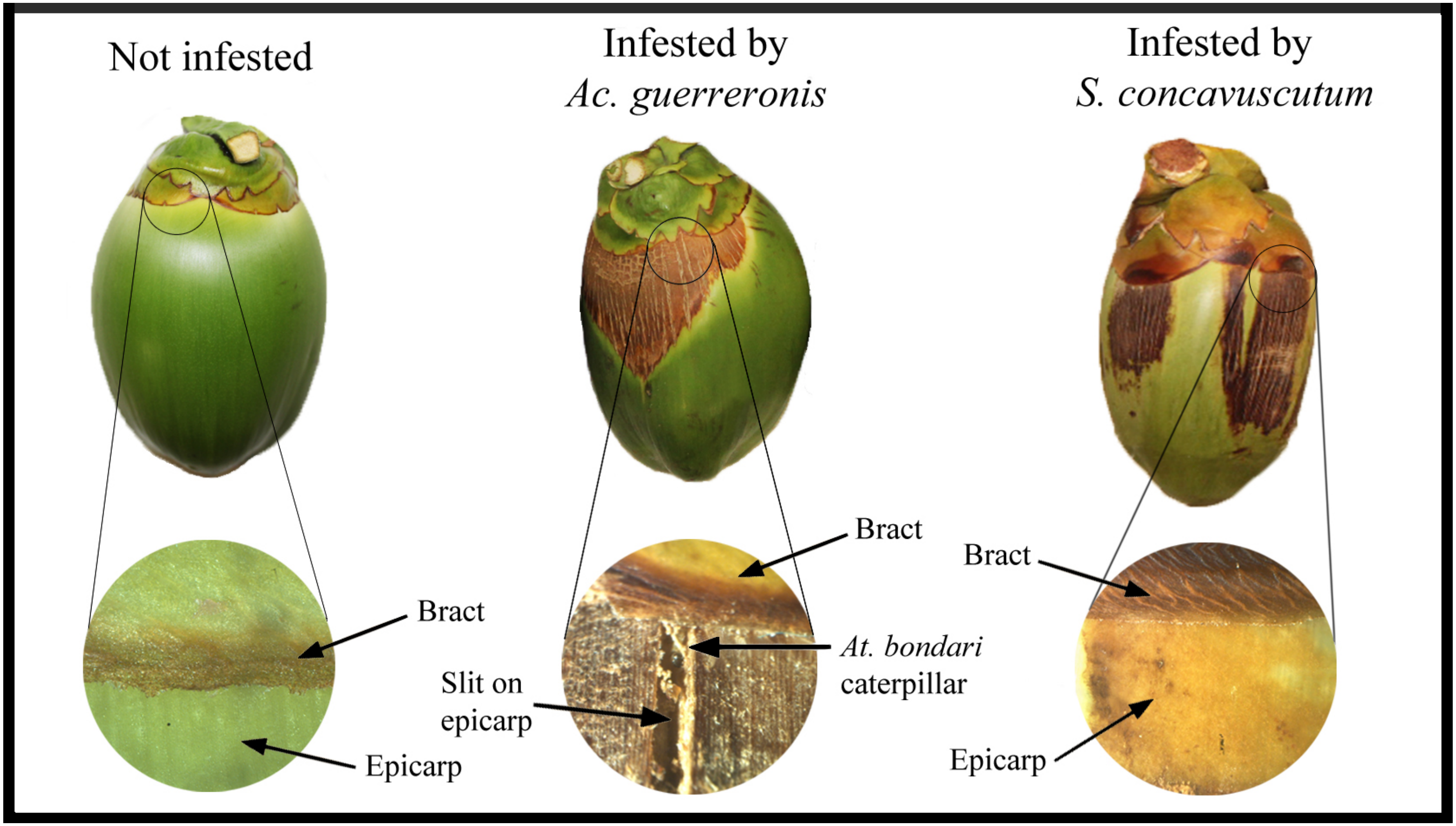


Figure 7. Image of coconuts either infested by *Ac. guerreronis*, *S. concavuscutum* or not infested, highlighting the place where the caterpillars access the meristematic zone. *Atheloca bondari* caterpillar using the slit caused by the injury of *Ac. guerreronis*.

Figure 8. Image of coconuts 5 days after the colonization of *At. bondari* caterpillars. **(A)** *Ac. guerreronis*-infested nuts. **(B)** *S. concavuscutum*-infested nuts. **(C)** non-infested nuts.

CAPÍTULO 5

FINAL CONSIDERATIONS

This study shows that *Atheloca bondari* is the species of occurrence in Brazil, different from what has been previously reported. In addition, the genetic variations between *At. bondari* and *At. subrufella* support the idea of two distinct species.

Necrosis caused by *Aceria guerreronis*, facilitates the access of *At. bondari* to the meristemmatic region of coconut fruits. Nuts with injuries caused by *Steneotarsonemus concavuscutum* do not show a high infestation of *At. bondari*. Field data show that the infestation of *At. bondari* can potentiate the abscission of coconut fruits, however, a complementary study isolating the infestation factors is necessary for a conclusive result. Besides that, we recommend studying the preference of oviposition for fallen nuts.

Aceria guerreronis-infested nuts improved the fitness of *At. bondari*, besides influencing moth preference. Although *At. bondari* is reported as a pest of economic importance in some situations (semi-extractive production). We highlight that the importance of *At. bondari* as a coconut palm pest is limited by the presence of *Ac. guerreronis* in the nuts.

Throughout the articles we suggest some studies. I point out some here: (1) to evaluate the fallen and vigor of nuts attacked or not by *At. bondari* under different mite infestation criteria; (2) the difference in the nutritional quality of nuts under different infestation criteria; (3) effect of natural enemies on *At. bondari* behaviour.