Environmental Entomology, 46(1), 2017, 92–99
doi: 10.1093/ee/nvw152
Advance Access Publication Date: 6 January 2017
Research

Sampling

Judas Beetles: Discovering Cryptic Breeding Sites by Radio-Tracking Coconut Rhinoceros Beetles, *Oryctes rhinoceros* (Coleoptera: Scarabaeidae)

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Subject Editor: Francis Reay-Jones

Received 17 June 2016; Editorial decision 27 October 2016

Abstract

The coconut rhinoceros beetle, *Oryctes rhinoceros* L., is a serious pest of coconut and other palms throughout Southeast Asia and on several Pacific Islands. Adults damage and sometimes kill palms when they bore into the crown to feed. In contrast, larvae feed only on dead plant material at breeding sites. Typically, coconut rhinoceros beetle populations are controlled with a combination of biocontrol, pheromone traps, and breeding site removal. A field trial was performed at two locations on Guam to test the feasibility of using the Judas technique, releasing radio-tagged adults to discover cryptic breeding sites, for potential coconut rhinoceros beetle control. Of 33 radio-tagged beetles that were released, 19 were successfully tracked to landing sites, 11 of which were considered to be active or potential breeding sites, in five different microhabitats. The remaining 14 beetles were lost when they flew beyond the range of receivers. Only one of the radio-tagged beetles was caught in the numerous pheromone traps present at the release sites. Percent emergence weight (%EW, ratio of current/emergence weight) varied significantly by the microhabitat to which coconut rhinoceros beetles were tracked. When microhabitats were further grouped, the difference in mean %EW between the arboreal (74 ± 2%) and the soil-associated (82 ± 3%) groups were found to be highly significant. The %EW for coconut rhinoceros beetles that were successfully located (78 ± 2%) and those that were lost (72 ± 2%) also differed significantly. Radio-tracking coconut rhinoceros beetles shows promise as a method to identify cryptic breeding sites, which could then be treated, removed, or destroyed.

Key words: forest entomology, pest management, GIS, ecology & behavior, detection

The coconut rhinoceros beetle, *Oryctes rhinoceros* L. (Coleoptera: Scarabaeidae, Dynastinae), is a serious pest of coconut trees, *Cocos nucifera* L., and other palms throughout the Pacific and Southeast Asia. Adult beetles damage and sometimes kill palms when they bore into crowns of palms to feed on sap. Palms die when boring and feeding activities kill the apical meristem. Although coconut rhinoceros beetle damage does not always result in coconut tree mortality, the characteristic V-cut damage to palm fronds can adversely affect the nut production and the aesthetic value of ornamental trees (Hinckley 1973, Zelazny 1979, Bedford 2013).

Coconut rhinoceros beetle damage to coconut palms is caused only by adult coconut rhinoceros beetles feeding in crowns. In contrast, larvae cause no economic damage, as they feed on decaying vegetation at breeding sites, which include dead standing coconut palms, fallen coconut logs, rotting coconut stumps, and decaying wood of many tree species (Bedford 1976, 2013). Breeding sites are also found in piles of compost, sawdust, and manure where these materials are available. When coconut rhinoceros beetle breeding sites are abundant following damage from typhoons, war, or large-scale agricultural operations, a self-sustaining positive feedback loop may be initiated in which large numbers of coconut rhinoceros beetle adults kill large numbers of palms, creating new breeding sites that generate even more coconut rhinoceros beetles. This worst case scenario was observed in the Palau Islands when coconut rhinoceros beetles arrived near the end of World War II. A coconut rhinoceros beetle population outbreak was fueled by the availability of abundant breeding sites in the form of trees killed by military activities. Fifty percent of coconut palms were killed by coconut rhinoceros beetles throughout the Parlay Islands, and some of the smaller islands lost all of their coconut palms (Gressit 1953).

After feeding in the crowns of palms, adults of both sexes return to breeding sites, where they aggregate and mate, and females oviposit (Bedford 1980). Coconut rhinoceros beetle aggregation at breeding sites is facilitated by an aggregation pheromone produced by adult males (Hallett et al. 1995). The feeding–aggregation/mating–oviposition cycle generally repeats multiple times throughout the lifetime of adult beetles (Gressit 1953). Vander Meer (1987) developed a body mass index, percent emergence weight (%EW), which is strongly correlated with the physiological and behavioral status of coconut rhinoceros beetle adults.

Coconut rhinoceros beetle was first detected in Guam in the Tumon Bay tourist hotel area in September, 2007. A delimiting survey indicated that the infestation was restricted to only a small region of the island (<500 ha) and an eradication project was launched (Smith and Moore 2008). The project relied on mass trapping using pheromone traps to capture adults and sanitation to remove rotting vegetation used as breeding sites. In addition, four detector dogs were trained to assist in finding breeding sites on the ground by sniffing out coconut rhinoceros beetle grubs.

Despite these efforts, coconut rhinoceros beetles damage in central Tumon Bay remained high and the infestation spread to all parts of Guam by 2010, making eradication impractical at that time. Attempts at population suppression using *Oryctes nudivirus* (OrNV), the preferred biocontrol agent for coconut rhinoceros beetles (Bedford 1986), also failed. It has recently been determined that the Guam coconut rhinoceros beetle population is genetically different from other populations in Asia and the Pacific, and it is considered to be a new invasive biotype of coconut rhinoceros beetles that is not subject to biocontrol by OrNV (Marshall et al. 2015). In addition to being resistant to all currently available isolates of OrNV, it appears that the coconut rhinoceros beetle-Guam biotype behaves differently. Coconut rhinoceros beetle breeding sites are commonly found in coconut palm crowns on Guam (Moore et al. 2015), but arboreal breeding sites are found only occasionally in other areas where the beetle occurs.

Eradication of coconut rhinoceros beetles from an island is difficult once this pest has become established. On two islands in Fiji, mass trapping using the now superseded synthetic attractant ethyl chrysanthemate coupled with sanitation from 1971 through 1974 failed to eradicate coconut rhinoceros beetles (Bedford 1980). The only proven tactic for eradication is a vigorous sanitation program that discovers and destroys all active and potential breeding sites. The single successful coconut rhinoceros beetle eradication to date was accomplished during the 1920s on the tiny (36 km^2) Niuatoputapu Island (also known as Keppel Island), which lies between Samoa and Tonga, using sanitation alone (Catley 1969, Bedford 1976). Given the importance of finding and destroying breeding sites in coconut rhinoceros beetle eradication and the inherent difficulty of locating breeding sites, which are often cryptic and are found in a wide range of locations (Hinckley 1973, Bedford 2013), there is a pressing need to develop detection methods to reliably find these sites.

Potential agents for detecting pest species include predators, parasitoids, and conspecifics of pest animals, which have often evolved behaviors and superior sensory systems that aid in finding either prey or mates in a complex natural environment. An example is the use of the predatory wasp, *Cerceris fumipennis* Say, a natural predator of different beetles in the Buprestidae, to monitor the emerald ash borer (Swink et al. 2013). While *C. fumipennis* specializes on Buprestids, they are not a species-specific predator, capturing 52 different species in 11 different genera (Swink et al. 2013). A more species-specific monitoring technique is the use of "Judas goats," referencing the Biblical character Judas Iscariot, in the eradication of feral goat populations, particularly on islands (Taylor and Katahira 1988, Campbell and Donlan 2005). This technique involves fitting a Judas goat with a radio transmitter and releasing it into the wild to seek out other goats, which are then tracked and shot (Taylor and Katahira 1988). The Judas technique has been most commonly employed to control mammals (Spencer et al. 2015), but has also been used against fish (Bajer et al. 2011) and birds (Woolnough et al. 2006). Until recently, using the Judas technique with insects would have been impractical due to the relatively high mass of available transmitters. However, the recent development of lightweight, miniaturized radio-tracking transmitters now allows application of this technique to larger species of insect pests that aggregate in the wild.

Radio telemetry to monitor flying insects was first employed by Hedin and Ranius (2002) to study the dispersal range of the Russian leather beetle, *Osmoderma eremita* (Scopoli), and since then, several studies have adopted this technique to study the behavior of beetles. Large beetles in the Carabidae (Negro et al. 2008), Lucanidae (Rink and Sinsch 2007), and Scarabaeidae (Beaudoin-Ollivier et al. 2003, Ranius 2006, Hedin et al. 2008, Svensson et al. 2011, Chiari et al. 2013, McCullough 2013, Le Gouar et al. 2015) families have been successfully studied through radio telemetry. Of particular interest is the study by Beaudoin-Ollivier et al. (2003) that used radio telemetry to successfully describe the flight behavior of *Scapanes australis* (Boisduval), a rhinoceros beetle in the same subfamily as coconut rhinoceros beetle (Dynastinae).

Given that adult coconut rhinoceros beetles utilize semiochemical communication (and potentially other cues) to find mates and aggregate at breeding sites, this species offers a good opportunity to test the Judas technique with an insect. Coconut rhinoceros beetles equipped with radio transmitters, released into the wild, and then tracked have the potential to enable the location of cryptic breeding sites that could then be treated, removed, or destroyed. Herein, we report on a field trial to determine the feasibility of radio-tracking coconut rhinoceros beetles to find cryptic breeding site aggregations at two locations on the island of Guam.

Materials and Methods

Release Sites and Experimental Conditions

Tagged coconut rhinoceros beetles were radio-tracked after release at two locations on Guam: the War in the Pacific National Historical Park in Asan (13.465972° N, 144.710944° E; Fig. 1A) and the University of Guam Agricultural Research Station in Yigo (13.532444° N, 144.873333° E; Fig. 1B). Asan Beach National Park is roughly triangular with the ocean bordering one side, coastal wetlands on another, and forested hillside on the third. The park itself is a large, open, grassy field, and includes coconut palms on the edges, many of which displayed coconut rhinoceros beetle damage at the time of the study. The release site (144.708537° E, 13.473904° N) was at the middle of a large, grassy field. Barrel traps ($n = 16$) made from 45-gallon drums containing the coconut rhinoceros beetle pheromone oryctalure (Iriarte et al. 2015) were distributed throughout the park. The Yigo site is an inland agricultural experiment station farm bordered by residential areas and uncultivated forest areas that include coconut palms along with many other trees. At the time of the field trial, most coconut palms on the station were showing signs of coconut rhinoceros beetle damage. The release site (144.872750° E, 13.531333° N) was in the middle of an uncultivated field. Beetles were released in the vicinity of three types of

Fig. 1. The two release sites on Guam: (**A**) the War in the Pacific National Historical Park in Asan and (**B**) the University of Guam Agricultural Research Station in Yigo. Yellow dots mark the release sites (•), red triangles mark landing sites of radio-tagged coconut rhinoceros beetles (◊), and green arrows mark the last locations and headings lost coconut rhinoceros beetles (→). Initial tracking was conducted at night with landing locations confirmed the following day.

pheromone traps baited with oryctalure at this location: standard vaned bucket traps ($n = 3$ traps; Hallett et al. 1995), barrel traps made from 45-gallon drums ($n = 31$), and DeFence traps made from plastic netting that entangles the coconut rhinoceros beetles ($n = 4$; Iriarte et al. 2015). Thus, both sites feature relatively accessible terrain that provides a variety of potential breeding sites as well as adult food sources.

Weather conditions during the experiment were mainly clear with occasional periods of rain and overcast skies. Over the release period, August 8 to August 14, average temperature ranged from 27 to 29°C, whereas relative humidity was 80–88%. Beetles were generally tracked under clear skies with the exception of August 9 during which light showers occurred.

Collection, Selection, and Preparation of Test Insects

Coconut rhinoceros beetles used for radio-tracking were wild caught in barrel traps containing oryctalure and collected within 1 wk of capture. These beetles were placed in tubs containing moist peat moss, fed fresh banana slices, and allowed to rest for at least 3 d.

After the rest period, captured beetles were flight tested at least 1 d prior to experimentation. The flight test chamber consisted of a 121-liter lidded garbage container. Within the chamber, about 30 beetles were placed in a smaller open metal bowl half filled with moist peat moss atop an upside down 19-liter bucket. Beetles could only exit the bowl by flying out of it; therefore, any beetle found on the bottom of the flight chamber container the next morning was considered flight capable. Only coconut rhinoceros beetles capable of flight were selected for radio tagging and release. Flight-capable coconut rhinoceros beetles were transported and stored until release in lidded plastic bins ~45 by 30 by 18 cm containing 10–15 cm of damp peat moss. Some beetles remained in storage for up to 6 d prior to radio-tracking.

Flight-capable beetles were marked with a unique four-digit identification number engraved on one elytrum using a laser engraver (Fenix Flyer, Synrad Inc., Mukilteo, WA). The ID number, sex, mass, and elytral dimensions of each beetle were recorded.

With a hot-melt glue gun, a transmitter was glued to the pronotum of each beetle using ~250 mg of glue per beetle (Supp. Fig. 1 [online only]). Prior to transmitter attachment, the beetle pronotum was abraded with sandpaper to improve adhesion.

Tracking Equipment

Beetles were tracked using a radio receiver (model R410) equipped with a three-element folding Yagi antenna (model 13863). Two receivers operated in the 148.641–148.992 MHz frequency band and two operated in the 164.032–164.409 MHz band. The approximate detection radius for the telemetry system was 500 m.

Transmitters (A2414) had a maximum battery life of 45 d with a warranty guarantee of 22 d. Each transmitter had a mass of ~300 mg. Transmitter frequencies for individual coconut rhinoceros beetles were recorded in conjunction with beetle identification numbers. All radio-tracking equipment was purchased from Advanced Telemetry Systems, Isanti, Minnesota. Handheld GPS units (Garmin Oregon 650, Salem, OR) were used to record locations where beetles were found or point of signal loss for each beetle.

Beetle Release and Tracking Procedure

Beetles were transported to release sites in plastic storage bins. The lid of the bin was removed at dusk (roughly 19:30), and the container was closed at roughly 21:30. Once the containers were opened, coconut rhinoceros beetle activity was carefully monitored using an infrared camera (model E4, FLIR Systems Inc., Wilsonville, OR). Observation with the infrared camera revealed that the thermal profile of the beetles would change just prior to flight. Thermally active beetles observed emerging from the peat moss were briefly viewed under red light to record the identification number and determine the frequency of the radio transmitter. Though nearly all beetles flew independently, several beetles that had not yet flown by the end of experimentation were encouraged to fly by removing them from the peat moss and throwing them into the air to facilitate takeoff.

Coconut rhinoceros beetles were pursued on foot following release and were tracked until a landing site was determined or until the transmitter signal was lost. In either case, a waypoint was recorded at the landing site or the last point of signal reception using a GPS unit.

Landing sites were visited on the following morning, and attempts were made to more precisely determine the location of each beetle. Beetle locations were monitored over several days, and beetles and transmitters were recovered when possible at the end of the experiment. Coconut rhinoceros beetles and transmitters were successfully recovered by digging up beetles that buried into soil or compost; however, the locations of coconut rhinoceros beetles tracked to coconut crowns could not be as exactly determined due to the density of the frond foliage.

Analysis

In assessing the flight patterns of beetles for trends with respect to sex and size, percent emergence weight (%EW) was calculated. The %EW describes coconut rhinoceros beetle mass at the time of measurement relative to its estimated mass upon emergence as an adult. This value can be estimated based upon a linear equation relating elytral measurements and emergence weight (EW; Vander Meer and McLean 1975). This value is significant in data analysis because %EW reflects the present life stage of a beetle and how much stored energy it has available; coconut rhinoceros beetles emerge at their heaviest weight and gradually lose weight over their life span.

GPS coordinates of the release sites at both experimental locations as well as each coconut rhinoceros beetle landing site were displayed as X, Y data in ArcMap Version 10.0 (ESRI 2011). The distance between the release site and the location where each beetle was found was calculated by using the Point Distance tool in ArcMap.

Data were analyzed using SPSS Statistics software (IBM Corp. 2013) except where noted otherwise. All analyses of significance were made at the $P < 0.05$ level. All analyzed data were shown to be normally distributed by the Shapiro–Wilk test. Differences in weight, EW, and %EW means for coconut rhinoceros beetles that were successfully located or that were lost were compared with *t*-tests. The numbers of male and female coconut rhinoceros beetles that were successfully located or lost, as well as those tracked to above or below 1 m, were compared using Chi-square contingency tests with Yates correction. Linear regressions were used to analyze relationships between the distance beetles moved from the release point and beetle, weight, EW, %EW, and percent weight of the transmitter. Differences in the mean distance beetles moved at the two experimental sites and the mean distance male and female beetles moved were compared by *t*-tests.

Results

Tagging and radio-tracking of coconut rhinoceros beetles in this study led to the successful location of multiple cryptic breeding sites at both experiment locations. A total of 33 out of 34 beetles tagged for release flew during the course of this study. Of the 33 beetles that flew, 19 were successfully tracked to landing sites (Figs. 1 and 2). Most of coconut rhinoceros beetles tracked to landing sites were in tree tops (arboreal, $n = 11$), and the rest were on or below the ground (soil associated, $n = 8$).

Arboreal destinations were most commonly the crowns of coconut palms with coconut rhinoceros beetle bore holes; however, beetles also landed in the branches of other species of trees (Fig. 2). For

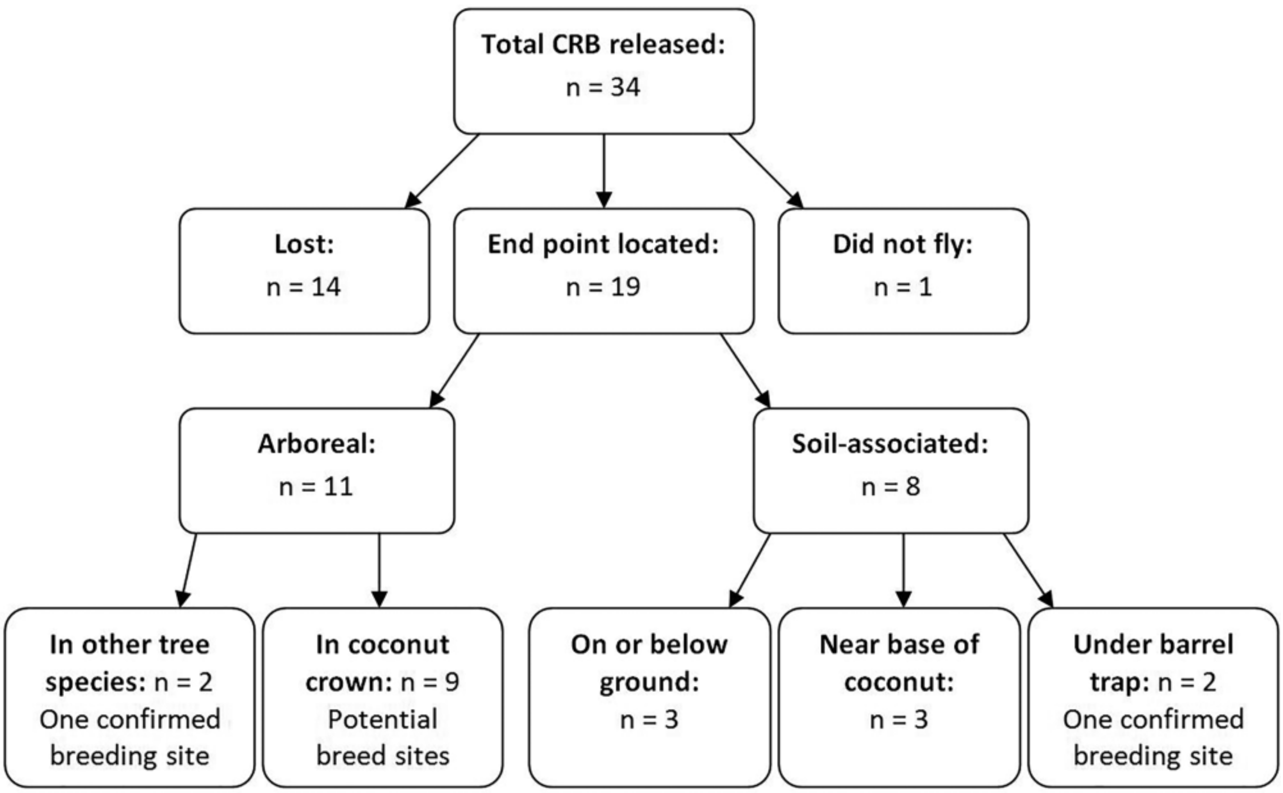

Fig. 2. Flowchart showing the fate of released radio-tagged coconut rhinoceros beetles (Judas beetles).

example, the first breeding site discovered by radio-tracking was in an extremely cryptic and unsuspected microhabitat: in a hole in a large rotting branch of a breadfruit tree (*Artocarpus altilis*) about 6 m above the ground. In this case, the transmitter became detached and the marked beetle was not recovered. However, three other coconut rhinoceros beetle adults and several larvae were found in the hole. It is highly likely that this breeding site was in a branch broken by high winds from Typhoon Dolphin, which passed over Guam in May 2015. In another instance, two beetles were tracked to the crown of the same highly damaged coconut tree independently of one another.

In soil-associated landing sites, coconut rhinoceros beetles tended to bury into the soil at depths up to ~15 cm upon landing. Typically, these sites were at the bases of trees. Four out of five of these landing sites were at the bases of coconut palms, though coconut rhinoceros beetles also landed in less predictable locations. For example, one beetle landed beneath a trailer parked on a grassy lawn in a residential area adjacent to the Yigo site. In two other examples of particular interest, single beetles were found beneath coconut rhinoceros beetle barrel traps baited with oryctalure at each experimental site. At the Yigo site, only the tracked beetle was observed underneath the barrel trap. At the Asan site, other beetles and larvae were also found beneath the barrel trap.

Of the 33 released beetles that flew, only one was captured in a pheromone trap. This beetle was released at the Yigo site on August 11 and was radio-located the following day in the crown of a coconut palm 336 m from the release site. During the trapping period running from September 4 through September 11, this same beetle was eventually caught in a barrel trap.

The mean trap catch rate of pheromone traps at the Yigo experiment station during August 2015 was 0.03 beetles per trap-day for standard bucket traps ($n = 3$ traps), 0.13 for barrel traps ($n = 31$), and 0.15 for DeFence traps ($n = 4$). In addition, no marked beetles were trapped in fish gill netting draped over a green waste pile at the Yigo site. This pile trapped 0.50 beetles per trap-day during August 2015.

Coconut rhinoceros beetles were most active from ~19:30 to 21:00, and flight activity did not appear to be heavily influenced by the prevailing weather conditions. Transmitters did not inhibit the flight mechanics of coconut rhinoceros beetles to an observable degree. Radio transmitters and adhesive accounted for between 8.5 and 17.8% of the coconut rhinoceros beetle weights at the time of release. There was no statistically significant correlation between coconut rhinoceros beetle flight distance and increasing percent transmitter/adhesive weight (as a ratio of total beetle weight; $R^2 = 0.048$; $y = 0.0004(4)x + 12(1)$; $F(1,17) = 0.864$; $P = 0.366$). Over the course of experimentation, it was observed that beetles warmed flight muscles to ~37°C directly prior to flight. This observation allowed a reliable prediction of when beetles were about to fly by detecting thermal radiation with an infrared camera.

Distance between release sites and landing sites ranged from 52.8 m to 564.6 m for the 19 beetles tracked to landing sites. The remaining 14 beetles, termed lost, were not specifically located either due to inaccessible terrain (coastal wetlands or private property, Figs. 1 and 2) or due to loss of radio signal. Mean displacement for both successfully located and lost coconut rhinoceros beetles could not be estimated, but median displacement for all released beetles was 333 m.

The %EW, 78 ± 2%, for coconut rhinoceros beetles that were successfully located differed significantly ($t(32) = 2.418$; $P = 0.021$) from coconut rhinoceros beetles that were lost, 72 ± 2%. However, EW ($t(32) = 0.226$; $P = 0.822$) and weight ($t(32) = 0.666$; $P = 0.510$) did not differ between coconut rhinoceros beetles that were successfully tracked or lost after release. Additionally, there were no differences in the numbers of male and female coconut rhinoceros beetles that were successfully located or lost ($\chi^2(1, n = 33) = 0.041$; $P = 0.839$).

No relationship was found between the distance beetles moved from the release point and beetle EW ($R^2 = 0.069$; $y = -0.003(2)x + 6.4(6)$; $F(1,17) = 1.252$; $P = 0.279$), %EW ($R^2 = 0.046$; $y = 0.01(1)x + 75(3)$; $F(1,17) = 0.824$; $P = 0.376$), or weight ($R^2 = 0.047$; $y = -0.001(2)x + 4.8(5)$; $F(1,17) = 0.829$; $P = 0.375$). There was no difference in the mean distance beetles moved at the two experimental sites, Yigo, 276 ± 42 m, and Asan, 215 ± 57 m ($t(17) = 0.848$; $P = 0.408$). Additionally, no differences were found between the mean distances male (246 ± 61 m) and female (258 ± 58 m) beetles moved ($t(17) = 0.370$; $P = 0.716$).

Landing locations of coconut rhinoceros beetles were categorized by microhabitats described as other trees, coconut crowns, traps, bases of trees, or soil unassociated with trees or traps (Fig. 3A). Microhabitats of coconut rhinoceros beetles were further clustered as arboreal (>1 m above ground) or soil-associated destinations (<1 m above ground; Fig. 3B). When microhabitats were grouped as either arboreal or soil-associated, the difference in mean %EW between the groups, arboreal, 74 ± 2%, soil-associated, 82 ± 3%, was found to be highly significant ($t(17) = 4.175$; $P < 0.001$). In addition, while EW was significantly different between arboreal, 6.5 ± 0.4 g, and soil-associated, 4.9 ± 0.5 g, microhabitats ($t(17) = 2.566$; $P = 0.020$), there were no differences in weight ($t(17) = 1.468$; $P = 0.160$) or distance traveled ($t(17) = 0.118$; $P = 0.908$) between these microhabitat groupings.

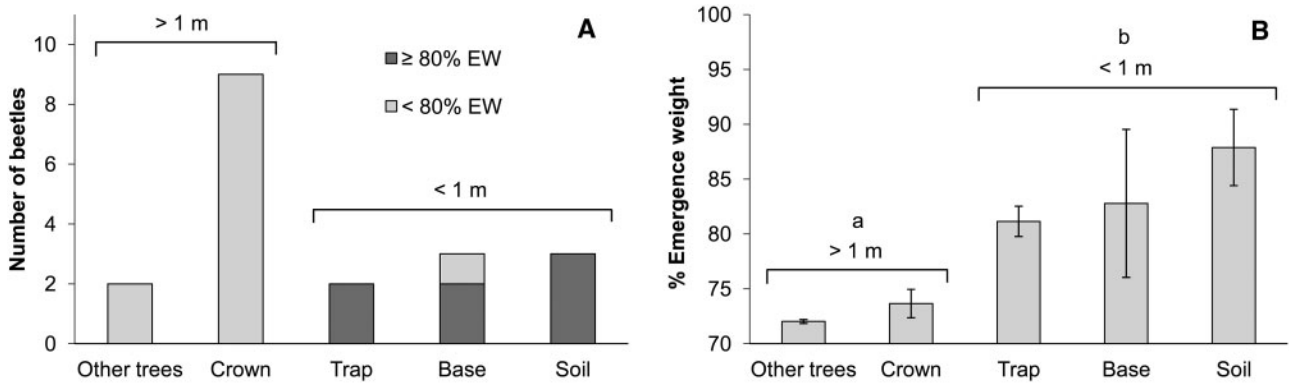

Fig. 3. Radio-tracked coconut rhinoceros beetles grouped by microhabitat of discovery location. (**A**) Numbers of beetles tracked to different microhabitats including an indication of percent emergence weight (%EW). (**B**) The %EW of beetles (mean ± SE) grouped by microhabitat. Lower case letters represent significant differences between beetles tracked to arboreal microhabitats (>1 m above ground) or soil-associated microhabitats (<1 m above ground; *t*-test, $P < 0.001$).

The numbers of male and female beetles did not vary between arboreal and soil-associated microhabitats ($\chi^2(1,\ n = 19) = 0.038$; $P = 0.845$).

Discussion

Radio-tagged coconut rhinoceros beetles (Judas beetles) were successfully tracked to cryptic breeding sites at two locations on the island of Guam. The two areas where coconut rhinoceros beetles were tracked differed both in topography and vegetation, and the effective location of tagged beetles in these different environments shows promise for the applicability of this technique in the varied habitats where coconut rhinoceros beetle infestations may occur. Out of 33 released coconut rhinoceros beetles, a total of 19 were followed to final landing sites while 14 beetles were lost.

The use of radio telemetry to monitor flying species has generally been constrained by the weight of radio transmitters. This limitation is especially true when monitoring flying insects because a small increase in weight may severely hinder flight behavior. In recent years, the gradual miniaturization of transmitters has circumvented this obstacle, allowing for more precise monitoring of flying insects (Kissling et al. 2014). One of the factors determining the feasibility of this study was whether adult coconut rhinoceros beetles could fly undisturbed with the attached radio transmitters. Adult coconut rhinoceros beetles are excellent fliers and can exert force much larger than their body weight when boring, so it was reasonable to expect that the miniature radio transmitters would have little to no effect on coconut rhinoceros beetles flight capability. Indeed, observed flight capability of coconut rhinoceros beetles was seemingly unaffected by the extra weight of radio transmitters. Radio transmitters plus adhesive amounted to no more than 18% of the coconut rhinoceros beetle weight at the time of release, and there was no correlation between the increasing percent transmitter/adhesive weight and the single flight distance of coconut rhinoceros beetles, indicating that coconut rhinoceros beetles could fly carrying the extra burden of the radio transmitters. It is important to note that the addition of the radio transmitters and adhesive resulted in only one coconut rhinoceros beetle experiencing a %EW of over 100%. This coconut rhinoceros beetle had a 110.64%EW once the transmitter and adhesive were included. These observations are consistent with other studies monitoring members of the Scarabaeidae family that found that radio transmitters did not noticeably affect beetle flight capabilities (Beaudoin-Ollivier et al. 2003, McCullough 2013).

There is little information available on the natural flight range of coconut rhinoceros beetles. In a laboratory experiment, Hinckley (1973) observed that tethered beetles attached to a flight mill flew between 2 and 4 km with flight duration of 2–3 h. However, field observations indicate that natural flight is limited to a few hundred meters, and this distance is influenced by the availability of feeding or breeding sites. Kamarudin et al. (2007) performed a mark-release-recapture study in a small (4.5 ha) oil palm replanting area containing a grid of 49 pheromone traps. Displacement averaged 118 m with a range of 51–186 m. The authors acknowledge that these values may be below the actual flight potential.

Another important factor to consider is the distance over which coconut rhinoceros beetles can be monitored. Radio telemetry monitoring typically covers only short to medium displacement distances, usually limiting the applications of the technology (Kissling et al. 2014). The radio devices employed in this study had an effective range of localization that varied with topological conditions. In this study, the range of detection was appropriate for monitoring, since the overall coconut rhinoceros beetle flight distance from release sites to landing sites ranged from 52.8 m to 564.6 m. This range also roughly delineates a radius for breeding site discovery from released coconut rhinoceros beetles; the Judas beetle must be released no further than ∼500 m from breeding sites. This might present difficulties for eradication teams since the breeding sites in question occur in cryptic locations presumably unknown to those searching for them. The relatively short detection radius of the radio devices obligates teams to close in on the cryptic sites through other investigative means.

Radio telemetry to monitor flying insects was first employed by Hedin and Ranius (2002) to study the dispersal range of *O. eremita*, and since then several studies have adopted this technique to study the behavior of beetles (Beaudoin-Ollivier et al. 2003, Ranius 2006, Rink and Sinsch 2007, Hedin et al. 2008, Negro et al. 2008, Svensson et al. 2011, Chiari et al. 2013, McCullough 2013, Le Gouar et al. 2015). Flight distance is the main metric that elucidates components of the behavior of interest. In this regard, coconut rhinoceros beetles fell within comparable mean distances but lagged in maximum flight distances compared with Rink and Sinsch (2007) reporting a maximum flight of 1,700 m and Beaudoin-Ollivier et al. (2003) reporting a maximum distance of 3,000 m. McCullough (2013) reported a maximum male flight of 402 m and a maximum female flight of 99 m but noted that most females flew out of range reaching up to 3,000 m of flight distance. This observation contrasts with coconut rhinoceros beetle flight patterns because the proportion of lost coconut rhinoceros beetles was not statistically significantly different between male and female coconut rhinoceros beetles.

Beetle microhabitat analysis was an integral component of these studies as well. McCullough (2013) was able to observe mating and feeding patterns, while Rink and Sinsch (2007) pinpointed final beetle locations to underground, ground level, and above ground, each representing different beetle behaviors. Beaudoin-Ollivier et al. (2003) utilized a combination of radio transmitters and enzymatic light tags to obtain even more detailed microhabitat observations. Radio telemetry also distinguished coconut rhinoceros beetle microhabitat selection patterns effectively, and the utilization of visual cues could increase the efficacy of this method in discovering cryptic breeding sites.

Radio transmitters with masses between 200 and 400 mg and detection ranges between 300 and 800 m have proved to be the most useful method to monitor large beetles. Such transmitters are light enough for undisturbed flight and provide sufficient coverage for monitoring beetles. Only one of these studies (McCullough 2013) expressed a substantial need for improvement in radio transmitter technology for the feasibility of beetle monitoring, while the remaining studies expressed the efficacy of the technique even over varied topographical conditions.

Despite the fact that all radio-tagged beetles were released within proximity of several different kinds of pheromone traps, including standard bucket traps, barrel traps, and DeFence traps, only one of these released beetles was trapped. Currently, a grid of pheromone traps largely covers the island of Guam, making it difficult to release beetles into areas where they are unlikely to encounter synthetic aggregation pheromone. Initial expectations were that pheromone traps might affect coconut rhinoceros beetle flight behavior and that many radio-tagged beetles might be trapped. However, somewhat surprisingly, large numbers of released coconut rhinoceros beetles were not caught the pheromone traps, showing that this technique may be compatible with monitoring and mass trapping efforts. If it is assumed that wild beetles respond to traps in the same way as radio-tagged beetles, it can be estimated that the suite of traps in the vicinity of the release points catches about one in 33 (∼3%) of wild beetles. This low trap performance is consistent with results from previous mark-release-recapture data from Guam (A. Moore, unpublished data). It is possible that oryctalure is less attractive to individuals of the coconut rhinoceros beetle-Guam biotype than it is to individuals of other biotypes. Results indicate that none of the currently available coconut rhinoceros beetle trapping methods are useful for population suppression of the coconut rhinoceros beetle-Guam biotype.

Although the majority of released coconut rhinoceros beetles were successfully tracked to discrete locations, 14 coconut rhinoceros beetles were lost presumably due to out-of-range flights. Interestingly, those coconut rhinoceros beetles that flew out of range had statistically significantly lower %EW than those that stayed within the detection range of the radio devices: $72 \pm 2\%$ compared to $78 \pm 2\%$, respectively, suggesting that lighter coconut rhinoceros beetles fly further from initial release site presumably in search of food sources. This observation raises the ability to minimize the loss of coconut rhinoceros beetles while radio-tracking. Prior to release, the %EW of coconut rhinoceros beetles must be monitored to ensure that the selected individuals will remain within the detection radius. The distance that found coconut rhinoceros beetles flew from the release site had no statistically significant correlations with %EW. However, the distance flown by all 33 coconut rhinoceros beetles that were released, both lost and found, could correlate with %EW if the distance of the lost coconut rhinoceros beetles were determined.

Moreover, %EW of released coconut rhinoceros beetles had a strong association with the microhabitats in which tagged coconut rhinoceros beetles were found. Of the 19 retrieved coconut rhinoceros beetles, 11 landed in arboreal microhabitats, whereas 8 landed in soil-associated microhabitats. Coconut rhinoceros beetles that landed in arboreal microhabitats had a statistically significant lower %EW than those coconut rhinoceros beetles that landed in soil-associated microhabitats, $74 \pm 2\%$ compared to $82 \pm 3\%$, respectively. In many locations studied, adult coconut rhinoceros beetles tend to split their time between feeding on the crowns of palms or breeding in either soil or compost (Zelazny 1975, Bedford 1980). As coconut rhinoceros beetles alternate between these microhabitats, individuals fluctuate in their %EW, making it possible to determine the behavioral pattern in which coconut rhinoceros beetles will engage by noting their %EW (Vander Meer 1987). Coconut rhinoceros beetles at a higher %EW will very likely refrain from further feeding and will instead fly in search of breeding sites, whereas coconut rhinoceros beetles at a lower percentage of their EW will likely forage in search for food. This corresponds with the observation that coconut rhinoceros beetles that landed in terrestrial microhabitats, commonly associated with breeding, had statistically significantly higher average %EW than those that landed in palm crowns, generally associated with feeding sites. This characteristic of the coconut rhinoceros beetle life cycle offers the potential that this tracking method be highly specific and controllable. In order to increase the probability that coconut rhinoceros beetles fly predominantly to soil-associated breeding sites, only individuals with a high %EW might be selected for tracking. In doing so, monitoring and eradication teams might improve the likelihood that the released coconut rhinoceros beetles will lead them to breeding sites rather than feeding sites, which will increase the effectiveness of this method.

It is important to note, however, that in Guam, coconut rhinoceros beetles are known to breed in both compost and coconut crowns (Moore et al. 2015), making it difficult to assess whether beetles are going to trees to feed or mate and making the distinction between arboreal and soil-associated microhabitats less useful in this specific location. At least one of the arboreal locations to which coconut rhinoceros beetles were tracked in this study, a damaged breadfruit tree, appeared to be a potential breeding site. Previous reports of coconut rhinoceros beetle breeding in coconut crowns on Guam were not from a random sampling but instead trees that showed coconut rhinoceros beetle damage and an accumulation of crown debris (Moore et al. 2015). However, in this study, all the coconut trees at the War in the Pacific National Historical Park in Asan were well maintained with minimal decaying organic matter in the crowns, suggesting that these beetles were more likely to be visiting coconuts to feed and not to breed. In contrast, several of the coconut trees to which coconut rhinoceros beetles were tracked at Yigo were not only heavily damaged by other coconut rhinoceros beetles but also had large amounts of decaying organic matter in the crowns. Therefore, these trees could be either breeding or feeding sites. In total, there were 10 landing sites in coconut palm crowns that might be potential breeding sites at the two locations. Due to limitations of time and equipment, the nature of beetle activity in coconut crowns was not further investigated, but this is an issue that could be taken up in future studies.

In terms of overall efficiency in time and materials, this Judas beetle method presents an effective technique that would improve existing control options for coconut rhinoceros beetles. Coconut rhinoceros beetle itself has several characteristics that lend themselves to the application of radio-tracking techniques with this species. First, it is a large, powerful beetle that can fly with the additional mass of a transmitter. Second, coconut rhinoceros beetle aggregates at breeding sites. And third, coconut rhinoceros beetles do not fly during the day, providing time to precisely locate landing points. Limitations of this technique encountered during this study include the cost of transmitters (~\$180 each) and the higher than anticipated number of lost beetles. Further refinement in tracking protocols and more experience for those tracking the beetles will likely lead to a lower percentage of lost beetles. Recapturing beetles in the field allows the reuse of transmitters and so a lower percentage of lost beetles also has the potential to reduce materials costs for a tracking program.

Beetle tracking to breeding sites required an input of ~30 min per coconut rhinoceros beetles immediately after release and about the same amount of time on the following day. The tactic of tracking coconut rhinoceros beetles to an approximate location during the night followed by more precise pinpointing during the daytime proved to greatly facilitate the retrieval of released coconut rhinoceros beetles, as it was much easier to visually track beetles and maneuver the terrain in the natural light of day. To further facilitate visual tracking, future experiments might include the use of small, lightweight LED lights in addition to radio transmitters.

Additionally, future experiments should consider the limitations of radio transmitter technology as they develop protocols for beetle tracking. In this field trial, the duration of commercially available radio transmitters (10–14 d) was appropriate for coconut rhinoceros beetle monitoring. Battery life of the transmitters is a major factor in determining monitoring protocol timelines. Therefore, in more extensive trials of this technique, experimenters should be aware of the time frame in which release and tracking should occur and must plan accordingly in order to achieve optimal coconut rhinoceros beetle tracking.

Future trials should also include visual monitoring of damage and trapping assessment of coconut rhinoceros beetle populations to effectively estimate possible locations of coconut rhinoceros beetle breeding sites. Based on such information for this trial on Guam, coconut rhinoceros beetle breeding sites clearly existed in the vicinity of chosen release sites. This protocol is particularly important in regions where coconut rhinoceros beetle is not yet widespread to ensure that tracking coconut rhinoceros beetles provides useful information. Once visual monitoring and trapping have indicated the existence of coconut rhinoceros beetles in a particular location, the Judas beetles would be released in the vicinity to pinpoint the exact location of the breeding sites. This combination of monitoring methods would ease the control and eradication of coconut rhinoceros beetles, and since traps and visual monitoring are already widespread, it would not be complicated to craft an integrated strategic plan. Regions in which coconut rhinoceros beetle is not yet widespread may also present concerns related to the introduction of additional coconut rhinoceros beetle adults. In this case, sterilized males could be used in tracking to prevent any potential impact upon existing coconut rhinoceros beetle populations.

This study was a success in that all but one of the 34 radio-tagged beetles flew, and the majority of these beetles were tracked to final landing destinations including definite breeding sites. In further assessing the final landing locations of beetles that were tracked successfully, it is important to note the varied and cryptic nature of these sites. For example, the breeding site found in the top of a breadfruit tree was well hidden within the leaves and branches and was ~6 m above the forest floor. This example demonstrates an unexpected site that would be nearly impossible to locate with current tracking methods such as trained dogs. Breeding sites discovered in other unusual locations such as beneath barrel traps or buried in the soil also demonstrate how tracking with conspecifics provides an advantage that cannot be rivaled by present tracking techniques.

Acknowledgments

Thanks to the USDA Forest Service for funding this project under grant 15-DG-11052021-205. Thanks also to Sheri Lee Smith, USDA Forest Service, to U.S. Park Service staff at the War in the Pacific Historical Park, and to Roland Quitugua and staff of the Guam Coconut Rhinoceros Beetle Project.

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

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