RECOVERY OF THE TERRESTRIAL CRAB *CARDISOMA CARNIFEX* AFTER BURROW DISTURBANCE

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Abstract. The importance of disturbance ecology grows as pristine habitat becomes increasingly encroached upon by land use change. This study focuses on the behavior of the burrowing terrestrial crab *Cardisoma carnifex* (Herbst 1794) on the island of Moorea after its semi-permanent burrow was disrupted. In the first manipulation, a set of four disturbance treatments was applied to burrows in sand and dirt substrate to examine recovery time. The second manipulation increased the intensity of the disturbance to see if the crabs' strategies change. The results showed a significant increase in recovery time with the intensity of disturbance in dirt substrates, but not in sand. There was also a significant combined effect of treatment and substrate type on recovery. The second set of data showed the same set of recovery strategies even as the disturbances were more intense. This shows that these crabs can restore their burrows in relatively low levels of disturbance, but it remains to be seen how they and other species cope with larger scale influences such as urbanization.

Key words: disturbance ecology; Cardisoma carnifex*; crustacean; recovery; burrowing behavior; Society Islands; French Polynesia*

INTRODUCTION

As the world becomes more influenced by development, organisms are faced with the constant requirement to adapt their behavior to their changing surroundings, i.e. human activities such as landscaping, sediment displacement, and other forms of habitat alteration. These disturbances lead to stress, quantifiable as perturbations by Rykiel (1985), or deviations from an environment's 'nominal state' (Odum 1979). With the former equilibrium interrupted, new coping strategies may arise. In order to quantify these new strategies, organisms must be examined as displacement occurs and they react to a disrupted environment.

Organisms that create semi-permanent structures within their habitats are optimum subjects for these kinds of observations. Burrowing animals such as terrestrial crabs are particularly sensitive to land use changes (Lucrezi *et al*. 2009). Their burrows can be subject to disturbances of both natural and anthropogenic causes. Due to its proximity to picturesque ocean views, crab habitat is often paved over or landscaped for developmental purposes. The soils are compacted for roads, covered in new substrate, or even excavated during foundation building. The crabs are constantly under pressure to restore their burrows in these changing conditions.

The terrestrial crab *Cardisoma carnifex* (Herbst 1794) is particularly suitable as a model system to study the effects of disturbance due to its ubiquitous burrows peppering coastline soils from East Africa to the Indo-West Pacific islands (Hartnoll 1988). These robust burrows can reach up to 2 m below the soil surface, terminating in a chamber at the level of the water table (Micheli *et al*. 1991). Studies have shown that these burrows remain inhabited by the same individual for its lifetime (Denhoy and Battersby 1992). While the lower chamber remains intact most of the time, the burrow entrances are often rebuilt every three weeks or so (Micheli *et al*. 1991).

On the island of Moorea in the Society Island archipelago of French Polynesia, *Cardisoma* burrows tend to cluster in loose soils underneath canopy cover near the coast (Elitzur 2001). The crabs groom the area around their burrow entrances, removing both of edible and inedible material leaving soils mostly bare save for the holes themselves (Bickel 1997).

This study examined how these crabs react to specific kinds of common disturbances, both those that would be seen naturally and those that are the result of human activity. By compromising the burrow entrances but leaving the rest of the burrow intact, the methods employed here mimic typical activities that only affect the surface of the soil such as gardening, path landscaping, and rock displacement. By repeating disturbance treatments, recovery time and relationship to original burrow structure was examined. Recovery within a week was predicted for all the burrows, with faster recovery in sandy substrates. I also expected the crabs to evade the disturbances if they were severe enough.

METHODS

Study site

This experiment was held on the northern side of the island of Moorea, French Polynesia (17° 30' S 149° 50' W), ranging from Gump Station to the base of the Opunohu Bay (Fig. 1, site coordinates in APPENDIX A).

Recovery time manipulation

I conducted walking surveys to find where burrows were clustered. Sites with closely clustered burrows were noted to

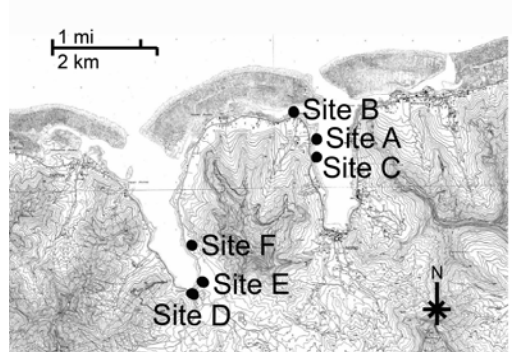

FIG. 1. Map of study sites, zoomed in on the northern coast of the island. Opunohu Bay is on the left, Cook's Bay on the right.

ensure the treated burrows at each site would have similar environmental conditions. I classified substrate type as sand or dirt via particulate size estimate; sand having a larger particle size and more pore space than dirt.

Six sites were chosen based on soil substrate and labeled with letters A-F. Groups of 12 burrows were chosen in three dirt soil sites (A-C) and three sandy soil sites (D-F), all within 30m from the shore. These groups of 12 were then split into three subgroups with four burrows each. The burrows were numbered one through twelve.

Four treatments were administered in such a way that each of three subgroups in the site contained a burrow receiving each treatment (Fig. 2). The four treatments were: (I) a control treatment with a small amount of crumpled paper placed in the entrance of the burrow to be dislodged in burrow activity, (II) a loose pack of soil, just enough to cover the entrance completely, (III) a tight pack of soil raked over the entrance and tamped down with the end of a hammer handle, and (IV) a rock cover large enough to be flush with the soil on all sides of the entrance. Burrows 1-3 received Treatment I, 4-6 received Treatment II, 7-9 received Treatment III, and 10-12 received Treatment IV.

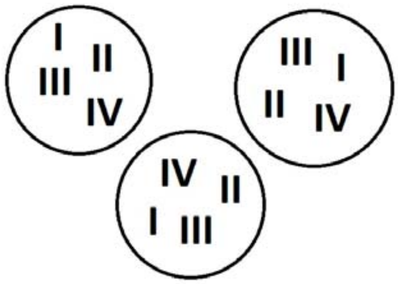

FIG. 2. Diagram of study site layout. Each of the three subgroups contains a burrow of each treatment: (I) control, (II) loose pack, (III) tight pack, (IV) rock cover.

Photos of the burrow entrance were taken with a Nikon D3100 DSLR camera just after administration including the treated burrow, the flag denoting the burrow number, and a six-inch ruler for scale (APPENDIX B). The burrows were visited each day and photos were taken with an index card denoting time lapsed once the burrow entrance was completely restored.

For each burrow I recorded the number of days elapsed until full burrow recovery classified as a completely cleared entrance, as well as burrow condition. The data and graphs were analyzed using the statistical package JMP 10 SAS Institute Inc. 2012. One-way ANOVA results were used to compare differences between the treatment recovery times in each substrate; two-way ANOVA results were used to see if recovery time differed between the substrates.

Intensive disturbance suite

In order to test how much disturbance it takes for a recovery strategy other than simply digging through the blockage or forming an exit chute, I set up three more treatments of more intense disturbance. This manipulation took place near Site A (dirt substrate). The three treatments were (V) filling the entrance to the soil surface with medium gravel, (VI) tightly packing the entrance with surrounding substrate and pouring one gallon of water on the soil to pack it further, and (VII) covering a set of burrows with a 1m by 1m piece of table slate. Fifteen new burrows were treated (1-5 receiving Treatment V, 6-10 receiving Treatment VI, and 11-15 receiving Treatment VII). Photos were taken of the burrows immediately after treatment and if there was evidence of recovery (APPENDIX C).

RESULTS

Recovery time manipulation

Of the 72 burrows treated, 66 recovered due to some site tampering or lack of activity over the study period, suggesting an empty hole. Thirty-four burrows were in dirt substrate and 32 were in sand substrate.

Dirt sites exhibited a trend in recovery times for the different treatments while sand sites did not show a clear trend (Fig. 3). In the dirt sites, as the treatment became more intensive the crabs took longer to rebuild the burrow entrance.

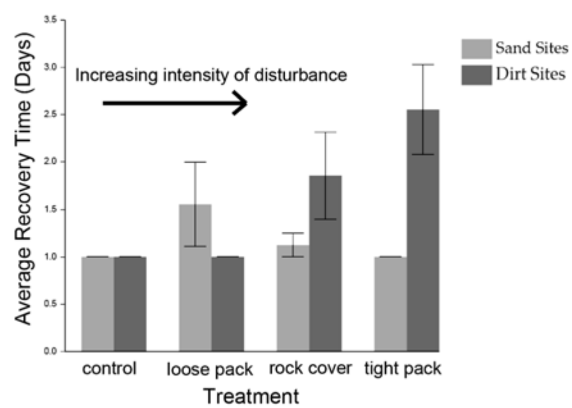

FIG. 3. Bar graph including average recovery times for each substrate. Significant attributes include the increasing recovery time in dirt substrates as the disturbance intensifies (ANOVA $F=6.0580$, $p=0.0045$) and the difference in overall average recovery times between substrates (ANOVA $F=4.7213$, $p=0.0052$).

The burrows in the packed dirt substrate were repaired in one to five days after disturbance. The recovery variances ranged from only one day in both the control and loose pack treatments (mean=1 day, n=9), one to four days in the rock cover treatment (mean=1.8 days, n=7), to one to five days in the tight pack treatment (mean=3 days, n=9), showing a clear upward trend related to severity of the treatment. There was a significant difference in burrow recovery time between treatments (ANOVA F=6.0580, p=0.0045).

Treated burrows in the sandy substrate were also repaired in one to five days, but the variances were one day in the control group (mean=1 day, n=9), one to two days in the rock cover treatment (mean=1.13 days, n=8), one to five days in the loose pack (mean=1.56 days, n=9), and one to five days in the tight pack treatment (mean=1.57 days, n=6). There was no significant difference between the recovery times of the treatments in this particular substrate (ANOVA F=0.7241 and p=0.5458).

As seen in FIG 1, the recovery times for the disturbed burrows differ between substrates. These differences were significant (ANOVA F=4.7213, p=0.0052). This shows a combined effect of treatment and substrate type on the time until the burrow was restored.

In condition, the burrow reconstructions were very close to the original structure (APPENDIX B). The crabs in 100% of the burrows filled with substrate dug out the plug as opposed to digging around tunnel blockage. In the burrows that were covered by rocks, 100% of the crabs dug out just enough soil to form a chute between the soil surface and the rock.

Intensive disturbance suite

Of the 15 burrows treated and recorded, 100% of them showed recovery that was similar to those of the main experiment. The crabs in burrows 1-10 (Treatment V and VI) dug through both the gravel and the mud pack in the original entrance position. Similar to the crabs in the rock cover treatment, burrows 11-15 (Treatment VII) had exit chutes leading to the edge of the slate (APPENDIX C).

DISCUSSION

In the timed recovery trials, the hypothesis of the burrow entrances being recovered within a week proved to be correct. The significant difference between the treatments in the dirt substrate suggests that as the blockage became more intensive, it took more time for the crabs to dig themselves out. This contrasts with the lack of difference between the treatments at sand sites, showing that disturbances from sand inputs were on a similar timetable to recovery. This is perhaps a result of the larger substrate size in sandy soils which increase air space, requiring less effort to displace. The burrows that were treated but not counted in the final results may change these trends slightly if the burrows were not empty from the start, but the timetable of the experiment and sample size prevented further investigation of these burrows that showed no activity whatsoever. Larger sample sizes in future manipulations will serve to better illuminate these trends.

The nature of the recovery was significant because all the crabs restored their burrows to be as close to their prior state as possible. As expected, the loose pack was quickly displaced since it was not a particularly destructive disturbance. This trend was particularly unexpected in the tight pack treatments where the crabs still kept the burrow entrance in the original position, even though the surrounding substrate was less tightly packed and thus easier to dig through. In the rock cover, the exit chute demonstrated a path of least resistance to restoring access to the burrow. In the intensive suite, the crabs followed the same behavioral pattern, moving gravel out of the burrow, digging through the packed mud, and building exit chutes to the edge of the table slate. Even as the disturbance was more of a challenge, the crabs still maintained their burrow to the best of their abilities. This entrance structure fidelity may be related to the rest of the burrow (i.e. tunnel orientation, crab size, territoriality). It may be the case that the crabs do not circumvent blockages because of spatial competition in highly populated soils (Aspey 1978). There may be an energetic reason for the original entrance location such as rocks or roots dictating where the burrow leads (Vleck 1978).

This ability to recover quickly from disturbance shows that *C. carnifex* is a species that will staunchly resist many kinds of low-level development by humans, as exhibited in its expansive range (Bishop 1986). Surface-level disruption such as landscaping, pathways, and rock displacement does not affect the soil near lower burrow structures as described by Micheli *et al*. (1991), so the crabs can easily continue to live through those events. However, as the holes crop up in the middle of gardens people will do more to prevent the 'destruction' of their property; deeper substrate disturbance or poisoning may be the next steps to prevent lawns from becoming riddled with extant burrows.

This and other arms races will continue to persist between people and the organisms that inhabit land slated for development. As technology and urbanization evolve, natural ecosystems must adapt to increasingly aggressive disturbance. Primitive dwellings and small townships can allow flora and fauna to coexist while cities and megascale agriculture set organisms farther back from their original state, in many cases preventing them from recovering at all. Continued research in these limits and tradeoffs is needed to find the line between land optimization and habitat preservation. Species ranges may shift into previously unfavorable environments, coping behaviors may change, or increasing inter- and intraspecific competition may reduce overall species fitness. Once these complex effects can be linked to causes, management and development practices can be implemented to maintain balanced economic and ecological values of the environment.

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APPENDIX A

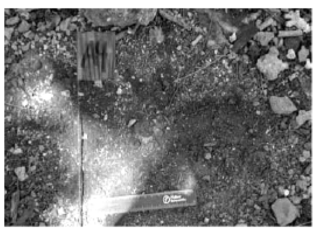
SITE	SUBSTRATE	GPS COORDINATES
A	Dirt	17° 29.282′ S, 149° 49.355′ W
B	Dirt	17° 29.747′ S, 149° 49.519′ W
C	Dirt	17° 29.332′ S, 149° 49.351′ W
D	Sand	17° 30.996′ S, 149° 50.966′ W
E	Sand	17° 30.943′ S, 149° 50.966′ W
F	Sand	17° 30.728′ S, 149° 50.979′ W

APPENDIX B

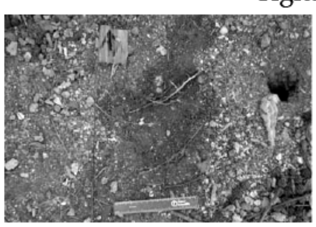
Disturbed Recovered

Control


Loose Pack




Tight Pack



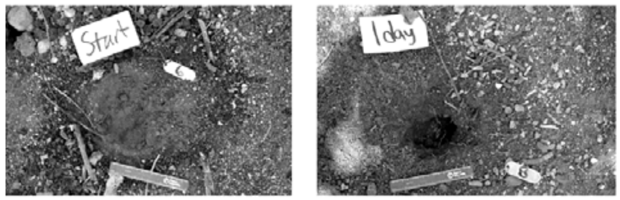

Rock Cover


APPENDIX C

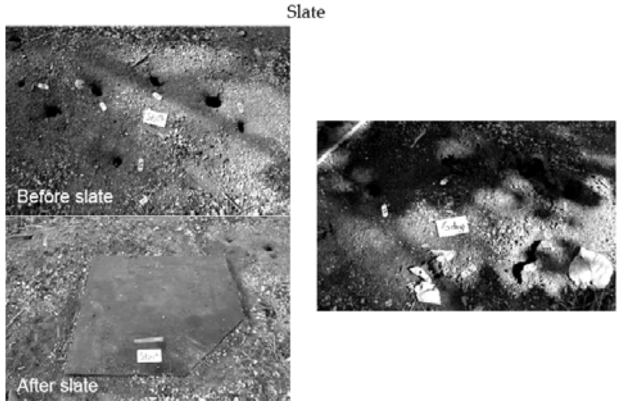
Disturbed Recovered

Gravel

Mud Pack

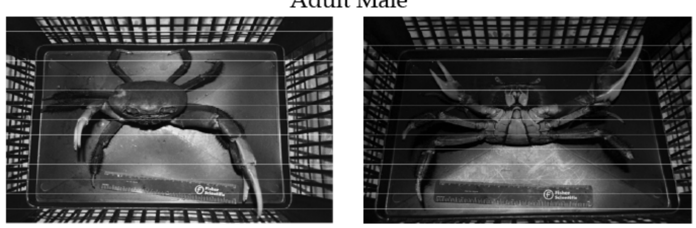


Slate

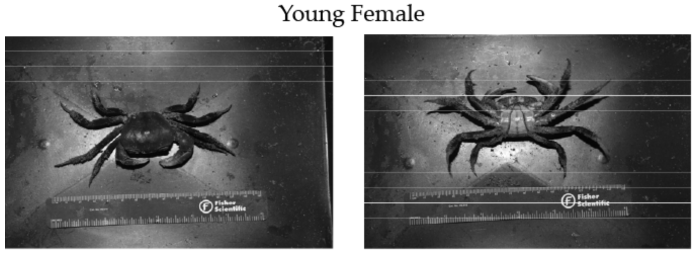


APPENDIX D

Dorsal Adult Male Ventral



Young Female



Six inch ruler for scale.