LAND SNAIL POPULATIONS IN ABANDONED WATER CISTERNS IN ISRAEL: A MODEL SYSTEM OF ARTIFICIAL NICHE COLONIZATION

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Abstract *Many untended water cisterns which had been in use until 68 years ago may be found throughout Israel. These cisterns constitute a unique ecological niche for a variety of organisms, providing a prime opportunity to explore the colonization of an artificial, little-studied ecological niche, over long periods of time. We actualized this approach by conducting a land snail survey in ten sites, and found colonization of cisterns by troglophilic species in six of them. We report for the first time the finding of live specimens of* Calaxis hierosolymarum *(Roth, 1855) in Israel, demonstrating the rare access to underground cavities provided by this study system.*

Key words *colonization, artificial niches, water cisterns, land snails, troglophilic land snails*

INTRODUCTION

Studying the mechanisms by which new niches are colonized and learning the time scales required for colonization to take place are paramount to understanding ecological and evolutionary processes (Turchin 1998; Nathan 2001; Bullock, Kenward *et al*. 2002). Particularly, such understanding is crucial for predicting the outcome of anthropogenically-induced environmental change and has practical implications on conservation efforts such as in attempts of habitat reconstruction and of reconciliation (Buckley 1989; Rosenzweig 2003; Lundholm and Richardson 2010).

Most of Israel's landscape is arid or Mediterranean. Traditional human settlement in the region was accompanied in the recent four millennia by the excavation of water cisterns to ensure water supply year round (Evenari, Shanan *et al*. 1982; Zartal 2001; Faust 2003; Faust 2005; Ackermann 2007). Many of these cisterns were in use until recently, and few are even in use to this day. Hundreds of such water cisterns are found throughout Israel, and many of them were in use until the state of Israel was established 68 years ago. Many of the cisterns continue to collect and hold varying amounts of water throughout the year, while others remain void of water but retain high levels of moisture year round (Palmach and Moran 1985; Markus 1993). The abandoned cisterns constitute a unique model system for the exploration of colonization of an artificial niche over 68 years, a relatively long period (cf. Ogden and Ebersole 1981; Turchin 1998; Van der Veken, Rogister *et al*. 2007, for discussions regarding the scarcity and importance of such studies). Notably, the cisterns are also unique in that they constitute cave-like underground cavities, an ecological niche which is in many cases hard to access and is little-explored in Israel (see, e.g., Culver and Pipan 2009).

Water cisterns constitute a death trap for a wide range of animals: frequently reptiles, mammals and arthropods fall into cisterns and, as a result of the bell-shaped structure of most of them, fail to climb out, finding their death in starvation or drowning. This is not so for land snails. They can easily scale smooth surfaces, regardless of their spatial orientation, and may thus take advantage of the unique, cave-like niche, which frequently remains moist throughout the dry season.

METHODS

In order to assess the extent of colonization of untended water cisterns by land snails and to identify the species which successfully exploit this niche, we conducted a survey of water cisterns throughout the years 2011 and 2012 in the Judean mountains and their western foothills, the Shefelah. Empty shells were collected from circa 30 cisterns and their epigean surroundings

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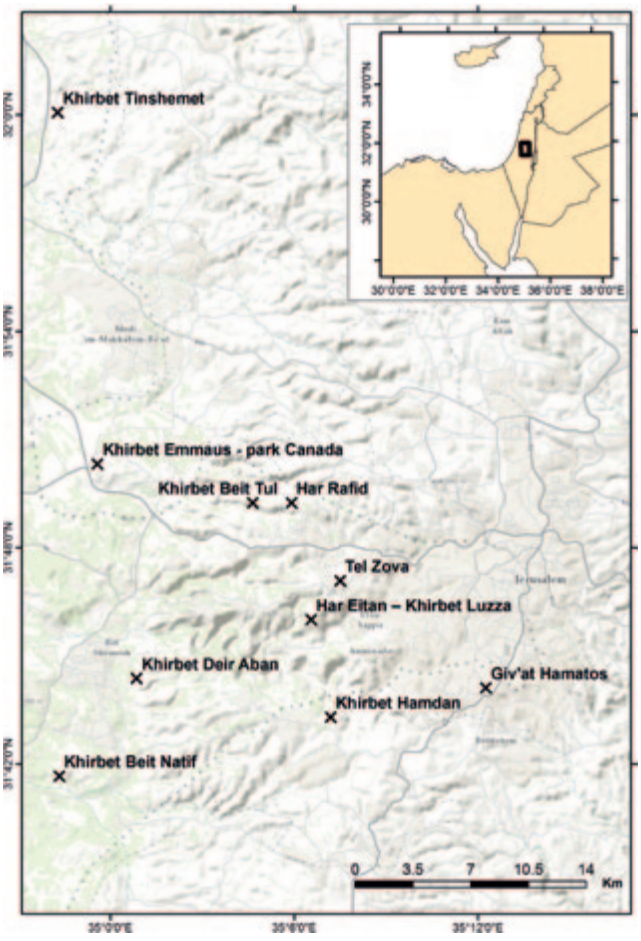

Figure 1 The location of the ten surveyed sites.

in 10 sites (see Fig. 1), and were subsequently identified to the species level. All identifications were confirmed by Henk Mienis, curator of the Israeli National Mollusc Collections (Hebrew University, Jerusalem, Israel; Tel Aviv University, Tel Aviv, Israel). We compared the species found within cisterns with those found in nearby epigean surroundings. This was done to differentiate between species whose shells were washed into the cisterns or occurred in them sporadically and species which had colonized the cisterns and maintain significant populations in them or which were found uniquely within the cisterns. The latter are henceforth referred to as 'colonizing species'. We also collected shells in nearby caves, where these were accessible, as these constitute the most similar natural habitat to that found in cisterns.

Active cisterns, which collect significant amounts of water and retain them year-round, may be viewed as a control regarding the state of snail colonization while the cisterns were in use. We did not find significant live populations of snails in any of the active cisterns which we examined. We attribute their paucity to the fact that the few surfaces that are not underwater are typically exposed and mostly unsuitable for permanent habitation by snails.

Results and Discussion

Shells of 21 species were found throughout our survey (see Table 1). Of these, 5 were found to be colonizing species (*Calaxis hierosolymarum* (Roth, 1855), *Calaxis rothi* (Bourguignat, 1864), *Calaxis saulcyi* (Bourguignat, 1864), *O*), *Oxychilus renanianus* (Pallary, 1939), *Pleurodiscus erdelii* (Roth, 1839); see Neubert *et al*. 2015 for a recent discussion of the *Calaxis* taxonomy in the region), and one species was found mostly in cisterns and caves but also sporadically under rocks and in crevices above ground (*Eopolita protensa (Férussac, 1832)*). Multiple live individuals (>30) of the species *C. hierosolymarum* were found in cisterns in Khirbet Deir Aban. Where natural caves are to be found in the vicinity, shells of all colonizing species were found in the caves as well as in cisterns, suggesting that local populations are the likely colonizers of the new niche.

All species which were found to be colonizing species are known to occur naturally in the region, and require humid environments (Kerney and Cameron 1979; Heller and Arad 2009). Three of the species (*Calaxis* sp.) which were found uniquely within the cisterns and caves are troglophilic species. *Calaxis* shells are known also from gravesites at archaeological digs (Heller & Arad, 2009). Otherwise, little is known about their ecology. They probably feed mostly on debris or fungi (Heller, Pimstein *et al*. 1991; Heller and Arad 2009; H. Mienis, personal communication, 2012). Cisterns remain dark and moist year-round, functioning as subterranean sinks of accumulating organic matter, providing a stable microbiome for subterranean fauna. Few live individuals of these three *Calaxis* species have been found in Israel so far (Mienis and Heller, personal communication, 2013), and our finding of live specimens of *C. hierosolymarum* in Israel is the first to be reported in the literature, to the best of our knowledge.

We found colonization of cisterns in most of the surveyed sites by troglophilic landsnails,

Table 1 Gastropod species found at each location site. Habitats within each site are denoted by Ci (cisterns), Ca (caves), AG (above ground). Species found primarily in cisterns and caves appear in bold.

	Khirbet Beit Natif (5 cisterns)	Khirbet Deir Aban (7 cisterns, 2 caves)	Khirbet Emmaus-park Canada (1 cave, 1 cistern)	Khirbet Tinshemet (4 caves, 1 cistern)	Khirbet Hamdan (1 cistern, 3 caves)	Giv'at Hamatos (3 cisterns)	Har Eitan – Khirbet Luzza (4 cisterns, 1 cave)	Tel Zova (3 cisterns, 3 caves)	Har Rafid (3 cisterns)	Khirbet Beut Tul (5 cisterns)
Buliminus labrosus spirectinus		AG			AG		AG	AG, Ca		AG
Buliminus labrosus labrosus							Ci	AG, Ca		
Calaxis hierosolymarum	Ci	Ca,Ci	Ca	Ca, Ci					Ci	Ci
Calaxis rothi		Ci								
Calaxis saulcyi	Ci			Ca, Ci						
Cristataria haasi kharbatensis				Ca, AG						
Eopolita protensa jebusitica	Ci	AG, Ci	Ci, Ca	Ca, Ci	Ca		Ci	Ca, Ci	Ci	Ci, AG
Euchondrus chondriformis				AG						
Euchondrus septemdentatus		AG	Ca, AG	AG, Ca	AG		AG	AG	Ci, AG	Ci, AG
Granopupa granum				AG						
Helix engaddensis	AG	AG, Ci		AG		AG	AG, Ci	AG		AG
Levantina spiriplana hierosolyma	AG	AG			AG	AG, Ci	AG, Ci	AG, Ci, Ca	AG	AG
Metafruticicola fourousi					AG					
Monacha crispulata					AG					
Monacha syriaca	AG	AG, Ci	Ci, AG, Ca	AG, Ca	AG, Ca		AG, Ci	AG, Ca, Ci	Ci, AG	AG, Ci
Oxychilus renianus							Ca	Ca	Ci	
Paramastus episomus		ci, AG			AG			AG, Ci, Ca	Ci	Ci
Pene sidoniensis					AG					
Pleurodiscus erdelli								Ca, Ci		
Sphincterochila cariosa		AG		AG			AG			AG
Xeropicta vestalis joppensis	AG	Ci, AG		AG	Ca, AG	Ci, AG	AG, Ci	Ca, Ci	Ci, AG	Ci, AG

Population sizes were not assessed in this survey. A species is recognized by a single shell or more occurring at a given site. A detailed account of the shells collected in each site and their distribution among the surveyed cisterns and caves is found in the Mollusca Collection in Tel Aviv University. All cisterns are very highly likely to have been in use until the establishment of the state of Israel, 68 years ago, and then abandoned. The cave and cistern in K. Emmaus may have been in use until more recently. In the two sites in which shells of *Eopolita protensa* were found above ground, they occurred there sporadically whilst occurring in great numbers (many dozens) within the cisterns.

Figure 2 Live *Calaxis hierosolymarum* (Roth, 1855), in a cistern in Khirbet Deir Aban.

Figure 3 One of the water cisterns surveyed in Khirbet Beit Natif.

which are typically thought to be slow dispersers. Moreover, they are usually found in ecologically stable sites with little seasonal turnover, suggesting that they reflect a faunal community that is no longer in its pioneering phase. This finding sets a time scale defining the colonization and the ecological succession processes occurring in these artificial habitats. It is particularly interesting in light of the perceived limitations on these species' long-distance mobility, influenced by their small size and sensitivity to epigean environmental conditions (cf. discussion in Aubry, Labaune *et al*. 2006; Heller and Arad 2009). One possible explanation may be that previously unobserved bursts of dispersal take place during the wet season, when above-ground levels of moisture allow it. Another possible explanation for this widespread colonization is the availability of habitable natural underground cavities in the limestone and chalk rocks which compose the Judaean Hills and their western foothills

Figure 4 One of the water cisterns surveyed in Khirbet Beit Tul.

(Heller and Arad 2009). Such cavities, despite being inaccessible to researchers, may constitute a means of safe dispersal of underground-dwelling organisms and intermixing of seemingly disjoint populations.

Conclusions

Water cisterns constitute an unusual speleological niche which has not been studied in Israel so far. Compared to the near-inaccessibility of most underground cavities, water cisterns lend themselves easily to exploration, and may help elucidate the unique features of subterranean habitats in semi-arid regions such as Israel. Our findings help to shed light on the time scale over which colonization and succession processes occur in artificial habitats, and highlight untended cisterns as a promising system for investigating these processes, especially since ecological research is frequently limited to relatively short time scales.

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