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Adaptive significance of arboreality: field evidence from a tree-climbing land snail

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Arboreality has evolved in a wide range of taxa, but its adaptive significance has rarely been examined in natural ecosystems. *Euhadra brandtii sapporo* is an arboreal land snail distributed in a restricted area of Hokkaido, Japan. We hypothesized that arboreality provides the species with significant survival advantages, which we tested via field observations and experiments. A monitoring census showed that *E. b. sapporo* hibernates in winter in the ground litter, climbs into the canopy in early spring and returns to the ground in late autumn. This seasonal movement appears to be effective for escaping from predation by ground-dwelling carabine beetles, whose activity was high during the summer based on a pitfall-trap census. Manipulative field experiments were conducted to compare survival rates in arboreal and ground-dwelling environments. We collected 120 *E. b. sapporo* individuals in summer and tethered 40 in tree canopies and 80 on the ground; half those on the ground were covered by baskets to prevent predation by large animals. The survival rate after 11 days was highest in the canopy, followed by that on the ground with a basket and was lowest on the ground without a basket. Predation was the main cause of death, but some died from other causes. Similar results were obtained in autumn, except for higher survival rates of the ground treatments. Analyses of carbon and nitrogen isotope ratios suggest that the land snail uses epiphytic lichens and mosses as food resources. In conclusion, arboreality has a marked advantage in reducing mortality in *E. b. sapporo* and is probably supported by food availability as well.

Forest canopies support an enormous amount of biodiversity. As much as 40% of nonmicrobe terrestrial biodiversity is estimated to exist within canopies (Novotny et al., 2002; Rodgers & Kitching, 1998). The species composition in canopies may be very different from that on the ground (Rodgers & Kitching, 1998; Schulze, Linsenmair, & Fiedler, 2001; Stork, 1988), including some of the most threatened of all terrestrial ecosystems (Stork, 1988). A wide range of taxa have been listed as canopy dwellers. As noted by Erwin (1982) in his estimation of global biodiversity, arthropods are some of the richest and most representative canopy species. In addition, mammals, birds, reptiles, amphibians, lichens, bryophytes, vascular plants, fungi and various other organisms utilize the space in canopies worldwide, forming complex food chains (Ellwood & Foster, 2004; Lowman, Schowalter, & Franklin, 2012; Ozanne et al., 2003).

Arboreality, representing a niche shift from ground to canopy environments, has evolved in numerous taxa, and it often involves marked changes in species' characteristics. For example, arboreal species tend to have unique morphology (Hirano, Kameda, Kimura, & Chiba, 2015; Ober, 2003; Raj Pant, Goswami, & Finarelli, 2014; Sheehy, Albert, & Lillywhite, 2016), anatomy (Fabre et al., 2013; Shattuck & Williams, 2010; Venkataraman, Kraft, & Dominy, 2013) and life history traits (Pizzatto, Almeida-Santos, & Shine, 2007) that are specialized for an arboreal environment. In a study of didelphid marsupials, arboreal species were shown to be superior in locomotive and manipulation ability on trees compared to taxonomically close ground-dwelling species (Delciellos & Vieira, 2009). Based on molecular phylogeny, the recent common ancestor of extant squirrels was arboreal, and flying squirrels are derived from it (Steppan, Storz, & Hoffmann, 2004). Accordingly, selection for an arboreal lifestyle is a window to further diversification in many terrestrial species.

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The driving factors of arboreality have been discussed by many authors. Theoretically, arboreal behaviour is adaptive when (1) the risks of predation (Healy et al., 2014; Shattuck & Williams, 2010), interference by competitors (Kimura & Chiba, 2010) or infection with diseases and parasites (Shattuck & Williams, 2010; Walker & Hughes, 2011) are lower in canopies than on the ground; (2) large food resources are available in canopies, or living within trees is efficient for hunting (Erwin, 1991; Kraft, Venkataraman, & Dominy, 2014); and (3) temperature, humidity and other environmental factors are more suitable in canopies than on the ground (Scheffers et al., 2013). Meta-analyses of mammals and birds (Healy et al., 2014; Shattuck & Williams, 2010) show that arboreal species tend to have longer life spans than ground-dwelling ones, suggesting that arboreality probably contributes to increased longevity. These arguments, however, have rarely been examined by direct observation in natural ecosystems. Does an arboreal lifestyle really provide survival advantages? If so, what factors are important in driving arboreal behaviour? More simply, why does a given species select canopy, not ground, as a habitat?

To answer these questions, we performed a series of field studies on the adaptive significance of arboreality. We focused on a tree-climbing land snail, *Euhadra brandtii sapporo*, which is distributed in a restricted area of Hokkaido, Japan. Although it is ranked as a near-threatened species (NT) in the national Red List (Ministry of the Environment, 2012), this species occurs at high density in undisturbed forests (Saeki, 2015). During the winter, *E. b. sapporo* hibernates in litter on the ground (Saeki, 2015), but it moves up into the canopy in the spring and moves down to the ground in the autumn. Based on our field observations, we believed that the species would be an ideal organism for examining the adaptive significance of arboreality, because it is relatively insensitive to the presence of humans, thus allowing us to observe its natural behaviour in the canopy. In general, land snails favour dark, humid and calcium-rich places (Azuma, 1982; Skeldon, Vadeboncoeur, Hamburg, & Blum, 2007). Thus, the canopy environment with its relatively light and dry conditions (Parker, 1995) and without any calcareous rock materials appears to be a poor environment for them. Nevertheless, arboreal land snails are found in many regions of the world (e.g. Hadfield & Saufler, 2009; Kasigwa, 1999), and *E. b. sapporo* is one such representative in Japan.

We assume that *E. b. sapporo* selects canopies as its habitat because arboreality brings considerable survival advantages. We aimed to identify these advantages by using three approaches. First, we observed the species' seasonal movement between canopies and the ground and characterized it in comparison with that of carabine beetles (Coleoptera: Carabidae: Carabinae), common ground-dwelling predators of land snails (Okuma, 1985). We predicted that the species would awaken from hibernation and move into the canopy when carabine beetles become active and climb down in autumn when beetles cease their activities. Second, we used manipulative field experiments to compare survival rates of individuals in arboreal and ground-dwelling environments. We predicted that survival rates would be higher in canopies than on the ground. Finally, we examined the feeding habits of *E. b. sapporo* by analysing carbon (C) and nitrogen (N) stable isotope ratios. Our expectation was that this species relies on food resources in the canopy, such as epiphytic lichens and bryophytes, rather than the ground litter on which ground-dwelling land snails generally feed (Mason, 1970).

METHODS

Study Area

Field studies and sample collections were conducted at the Tomakomai Experimental Forest (TOEF) of Hokkaido University, Japan. TOEF is located near the southern coastal margin of Hokkaido Island (42.68°N, 141.60°E), with an elevation range of 20–90 m. The climate of TOEF is characterized by cool summers and cold winters. The average annual temperature and rainfall are 6.7° C and 1112 mm, respectively (TOEF, 2016). Maximum snow depth in winter ranges from 20 to 50 cm. The area is within the cool-temperate deciduous forest zone. Dominant tree species are *Quercus crispula*, *Acer pictum* subsp. *mono*, *Acer amoenum*, *Tilia japonica* and *Magnolia obovata*. The topography is generally flat, with no steep slopes. Soil originated from volcanic ash, which was deposited when Mt Tarumae, located ca. 20 km away from TOEF, erupted about 330 years ago.

Seasonal Behaviour

To characterize the seasonal behaviour of *E. b. sapporo*, we monitored the number of individuals per unit land area in the canopy and ground litter from April to November 2014. For the collection of canopy data, we used three scaffoldings that were constructed at TOEF in 2003. The size and accessible tree species of the scaffoldings are listed in Fig. A1. These three sites were selected because our experience at these sites suggested that there would be sufficient individuals for phenological monitoring (Saeki, 2015). The sites are close together (i.e. with all three sites within a 1 km area) and had similar tree composition and management history. Once or twice a month, two or three persons climbed the scaffoldings and counted *E. b. sapporo* individuals within each of the cubic spaces surrounded by pipes. The land snails were commonly found on the bark and branches of mature trees. They naturally avoid metallic materials, and no individuals were observed on pipes during the investigation. At the same time, the density of *E. b. sapporo* in ground litter was investigated in three 5.4 m × 5.4 m plots. The plot area is the same as two of the scaffoldings described above. Each of the plots was placed 20–30 m from a scaffolding. Sampling intensity was set at 30 min/person/plot.

In addition, four pitfall traps (9 cm in diameter, 12 cm in depth, without bait and preservative) were placed approximately 20 m from one of the scaffoldings (SF4 in Fig. A1) from 29 April to 7 November 2014. Adult carabine beetles that fell into the traps were collected every 2–5 days, identified and counted in situ, and then released several metres away from the traps. We focused on carabine beetles because this taxon contains specialists that consume land snails; their predation was confirmed in the laboratory as well.

Two automatic interval cameras (TimelapseCam, Wingscapes, Calera, AL, U.S.A.) were set on one of the scaffoldings to record leaf phenology and the timing of disappearance of snow on the ground every day. The leaf flushing period was defined as from bud breaking to full opening of leaves, and the leaf-fall period started when the leaves changed colours and finished when no leaves were present in the canopy. Temperature and humidity were recorded by data loggers (TidbiT and HOBO U23 Pro v2, Onset, Bourne, MA, U.S.A.) set in the canopy (ca. 6–8 m height) and ground litter (0 m) at each scaffolding. Temperature was recorded from December 2013 to June 2015 and humidity from July 2014 to September 2015 at 2 h intervals. Unfortunately, one of the data loggers on the ground, set at scaffolding SF4, was damaged by animals, so we used the data from the other two for the ground temperature.

The abundance of *E. b. sapporo* in the canopy and of carabine beetles in the traps was converted into presence and absence data, and the relationship with temperature in the canopy was estimated using a generalized linear model (GLM). The activity of land snails is known to be affected by temperature (Staikou, Tachtatzis, Feidantsis, & Michaelidis, 2016). Hence, we assumed that temperature is a primary trigger of the seasonal movement of *E. b. sapporo*. Temperature on the ground was not used for the analysis because