Pathways for human movement are ubiquitous in most landscapes, including managed "wilderness" areas. For example, U.S. national forests contain 10% of U.S. road miles but only 8% of the land area (Forman and Alexander 1998). The effects of roads on wildlife populations are diverse and widespread, although most frequently studied near major urban areas (Gilbert 1989, Forman and Alexander 1998, Spellerberg 1998). It is known that roads are a source of introduced species, soil erosion, and various forms of pollution and disturbance. Moreover, roads lead to edge effects that spread into the surrounding habitat, resulting in altered microclimate and other disturbances. In addition, roads alter or prevent animal movement, possibly leading to habitat fragmentation and genetic divergence of populations (Selander and Kaufman 1975, Mader 1984, Reh and Seitz 1990, Forman and Alexander 1998). Between 15% and 20% of U.S. land area is affected by roads (Forman and Alexander 1998). For smaller and less mobile animals, narrow walking trails may have similar effects.

Small mammals, birds, frogs, turtles, beetles, and a snail avoid roads or trails (Baur and Baur 1990, Forman and Alexander 1998). However, it is not clear whether this avoidance is due to features of pathway habitats per se, preference for natural habitat, or avoidance of secondary disturbances associated with human use, as experiments have not been conducted. Correlative studies suggest birds avoid traffic noise (Reijnen et al. 1997) or poor food availability (Tabor 1974), while road salt may deter amphibians (Forman and Alexander 1998). Other possible causes of avoidance are various disturbances, pollutants, or predators (Forman and Alexander 1998). This study examines road avoidance and its proximate causes in the terrestrial land snail Oreohelix peripherica wasatchensis (Hemphill in Binney 1886), the Ogden Rocky Mountain snail. Movement preference relative to pathways was assessed in the field, while habitat features causing pathway avoidance were assessed with laboratory choice studies.

The oreohelicid snail O. p. wasatchensis occurs in a 17-ha area in the Wasatch Mountains 1 km south of Ogden Canyon (Fig. 1) in Ogden, Utah (41°14′N, 111°55′W; altitude 1310–2020 m). It is a hermaphroditic, pulmonate snail that feeds on vegetation and detritus and lives under leaf litter (usually maple) and/or limestone or quartz rocks (Pilsbry 1939, Clarke 1993, personal observation). The main snail habitat is a normally dry draw that runs approximately east to west upslope. Vegetation is mostly bigtooth maple (Acer grandidentatum). A largely treeless area within 100 m either side of the main draw also contains O. p. wasatchensis under scattered patches of bigtooth maple, sagebrush (Artemisia tridentata and A. ludoviciana), and a variety of small shrubs. Two U.S. Forest Service trails cross the study area, as well as 2 dirt access roads for public utilities and numerous unnamed trails increasingly frequented by hikers, joggers, and mountain bikers.

Four sites were chosen for the study: 2 near pathways and 2 control sites away from pathways (Fig. 1). One pathway site is along the eastern edge of the upper road (which is 5 m wide), while the 2nd is along the southern edge of a trail (0.7 m wide). Test snails were gathered from downslope of the study sites in
summer 2000. At each site 30 randomly selected and individually marked snails were placed in 2 parallel 4-m-long lines which were 25 cm apart and paralleled the pathway, with one line of snails directly on the edge of the pathway. Stakes were placed every meter to establish a baseline axis for movement measurements. Initial snail positions were recorded using x-, y-coordinates from this design. The next day I again recorded positions of all recovered snails to the nearest centimeter. Snail movement direction was determined trigonometrically. The 0–180° axis of movement was parallel to the nearby pathway rather than being absolute direction. Preferred movement angles between 0° and 180° thus signify movement away from pathways. For control sites the 0–180° axis was arbitrary. Rayleigh’s test (Zar 1984) was used to test angular direction preference (φ) at each site.

To determine whether pathway avoidance was related to habitat features per se, I conducted choice tests in the lab using 25 × 17 × 8-cm terraria. Test substrates were gathered from the natural snail habitat. Half of each terrarium was filled 4 cm deep with one test substrate and half with the other. I used the following substrate combinations: (1) natural snail substrate plus leaf litter versus road material, (2) natural snail substrate alone versus road material, (3) wet natural snail substrate versus dry natural snail substrate, (4) road substrate plus leaf litter versus natural substrate, (5) natural substrate plus dry leaf litter versus dry natural substrate without litter, and (6) natural substrate plus artificial leaves (Michaels Crafts Inc., stock number 5517300999) versus natural substrate. A snail was placed in the center of each terrarium, after which both substrates were equally watered (unless wetness was a choice factor). Temperature was 21–24°C with a 12:12 light:dark cycle. The snails were then given 24 hours to make a habitat choice. A second 24-hour trial was then run using the same snail but with substrates switched 180° to control for environmental gradients. The data for each snail thus consisted of the results of 2 trials per substrate combination. In any test each individual could have consistently chosen one substrate or the other, or had a mixed preference. Chi-square tests were used to determine whether the distribution of these outcomes differed from chance for sets of 12 to 17 snails tested with each substrate combination. Snails were reused in different tests but not within the same test.

Control site snails had no directional movement preference (site C1: n = 13, Z = 0.4, P > 0.5; C2: n = 16, Z = 1.9, P > 0.10), while road and trail site snails moved away from pathways (road: n = 12, Z = 6.0, P < 0.002, φ = 95.2°, trail: n = 23, Z = 10.0, P < 0.001, φ = 102.5°).

Snails preferred natural substrate with leaf litter to road material (n = 12, χ² = 22.0, P < 0.001), but they showed no preference between natural substrate and road material (n = 15, χ² = 1.8, P > 0.05). There was no significant preference for wet vs. dry natural substrate (n = 17, χ² = 1.0, P > 0.05). There was a significant preference for natural substrate with dry leaf litter over natural substrate without litter (n = 15, χ² = 30.5, P < 0.001), as well as for leaf litter on road substrate over natural substrate alone (n = 13, χ² = 31.5, P < 0.001). Natural substrate with artificial leaves was preferred to natural substrate alone (n = 15, χ² = 31.0, P < 0.001), and natural substrate with artificial leaves was preferred to any other substrate (n = 13, χ² = 22.0, P < 0.001).
chosen over natural substrate alone \((n = 14, \chi^2 = 8.2, P < 0.05)\).

The field and experimental results show that \textit{O. p. wasatchensis} avoids areas without leaf litter. The first choice test showed preference for natural substrate and/or avoidance of road substrate. The only secondary effect of pathways not eliminated by this test was soil pollution. However, the snail did prefer road substrate if it was covered with leaf litter, and so avoidance of pollutants is unlikely. The first choice test also does not show whether the snail’s preference is for natural substrate or for the effect(s) of learning or food availability, predator protection, shelter, and/or extra moisture retention provided by leaf litter, and thus does not discern the primary factor in natural substrate preference. The lack of preference in the test involving natural snail substrate without leaf litter versus road material, and the significant preference for leaf litter on road substrate over natural substrate alone, suggest that it is some quality provided by leaf litter that is most important to snail habitat choice. Thus, pathway avoidance appears to be a function of preference for leaf litter. The definitive field experiment of adding leaves to pathways was attempted twice, but trail users destroyed it.

The lack of preference for wet versus dry natural substrate and the preference for dry leaf litter versus no leaf litter when both were on natural substrate suggest that substrate moisture or leaf moisture retention are not the main proximate factors that affect preference for leaf litter. Furthermore, the preference for artificial leaves suggests that shelter and cover are important factors in snail habitat choice. However, I cannot completely rule out the role of leaf litter as a food source, since the artificial leaf test results were barely significant in comparison to other tests, and because it is difficult to completely eliminate potential food using artificial leaves.

Although Baur and Baur (1990) found pathway avoidance in the field in the European snail \textit{Arianta arbustorum}, they did not isolate the proximate factors involved. Baur (1986) did find that slope affected movement preference in \textit{A. arbustorum}, but slope probably did not affect my results since all study sites had similar inclinations. Goodfriend (1983) found that the snail \textit{Cepaea nemoralis} moved upwind, but this factor is also unlikely here since my sites experienced similar wind direction.

My results imply that pathways create barriers to movement in this species. Consequently, this snail’s habitat may be fragmented by pathways into numerous subpopulations that may be genetically divergent, as has been shown for other snails (Selander and Kaufman 1975) and frogs (Reh and Seitz 1990). Consequently, these subpopulations may fluctuate more widely in abundance and with a higher probability of extinction (Soule 1987, Opdam et al. 1993, Schilthuizen and Lombaerts 1994). This may be a major threat to \textit{O. p. wasatchensis}, which only occurs at this location and is a U.S. candidate endangered species and Utah Species of Special Concern. Future research should explore this possibility.

C. Meadows and M. Morin helped develop the sampling protocols, and S. Linssen did the GPS mapping. L. England and S. Zeveloff provided valuable comments on the material that formed the basis for this work.

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*Received 20 November 2000
Accepted 13 June 2001*