ROAD SURVEYS FOR TURTLES: CONSIDERATION OF POSSIBLE SAMPLING BIASES

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Abstract.—Herpetofaunal surveys often rely on observations obtained via road cruising. The ease with which many species of amphibians and reptiles can be observed on roads makes this a useful technique. However, road surveys have inherent limitations and biases, particularly for turtles. Observations of turtles along roads are likely biased towards large, adult female freshwater turtles on nesting forays and male terrestrial turtles that typically have a large home range. Turtles may also use roadsides as habitat and their presence on roads may not necessarily be reflective of their abundance in adjacent natural habitats. Researchers who use road surveys to examine demographic parameters of a turtle population (e.g., sex ratio or age class structure), or to describe a turtle community (e.g., species richness) should consider these biases in their conclusions and explicitly note the role of road cruising in data collection.

Key Words.—road cruising; road survey; sampling technique; spatial ecology; tortoise; turtle

OVERVIEW

Road surveys have been used to monitor the populations of a wide variety of taxa (e.g., Ashley and Robinson 1996; Goosenn 2000). This technique has been used primarily to determine road mortality rates of birds and mammals, and biases of this methodology have been identified for these groups (e.g., Rolley and Lehman 1992; Loughry and McDonough 1996). Road surveys have also been used in similar ways to describe amphibian and reptile communities (Fitch 1949; Kauffeld 1957) and are effective to observe a diverse array of squamates (Rodd 1990; Bernardino and Dalrymple 1992), chelonians (Haxton 2000), anurans (Hels and Buchwald 2001) and caudates (Mazerolle 2004).

Unlike in avian and mammalian studies, herpetological surveys often use observations of living and dead amphibians and reptiles on roads to make inferences about populations. Amphibian and reptile road survey data have been used to document the status of populations (Busby and Parmalee 1996), identify activity patterns (Henke and Montemayor 1998) and to quantify species diversity (Turner et al. 2003) as well as road mortality rates (Ashley and Robinson 1996; Smith and Dodd 2003). Although biases of other sampling methodologies have been identified for reptiles (e.g., Ream and Ream 1966; Prior et al. 2001) and amphibians (Dodd 1991), an evaluation of the inherent biases and limitations of road surveys has yet to be thoroughly discussed.

There are several aspects of road surveys that make them attractive to researchers. Driving roads is not labor intensive and allows the observer to cover a large area relatively quickly. The open areas on the road and the road shoulder provide opportunities to observe wildlife which may otherwise be obscured by vegetation or other landscape features. Furthermore, road surveys may be an effective tool for locating species that are difficult to trap and otherwise record such as aquatic snakes (Bernardino and Dalrymple 1992) and fossorial or cryptic species.

The magnitude of amphibian and reptile road mortality has been well documented (e.g., amphibians and snakes, Dodd et al. 2004; and turtles, Aresco 2005a) and carcasses collected on roads may serve as an important source of museum specimens. Road-killed animals can be useful for obtaining ecological and life history data such as geographic distribution, morphology, reproductive condition, and dietary components, for example, of a particular species (e.g., Case 1975).

THE ROAD SURVEY TECHNIQUE

Road survey methods (road cruising) are straightforward. The road serves as a transect and the number of organisms encountered on a specified route is expressed per unit time or distance (e.g., kills per km). Ideally, the speed of travel is standardized and is slow enough that most individuals of the target taxa are observed and identified. The number of observers should also be consistent, as the total individual animals detected along the road will likely be influenced by the effort invested. Furthermore, observer experience should be standardized as much as possible. If target species are particularly small it may be necessary to conduct counts on foot (Enge and Wood 2002).

Efforts should be scheduled such that they incorporate patterns of activity, with an emphasis on whether the target organism is nocturnal, diurnal or crepuscular. Animal movements may also be highly seasonal. For example, snake migrations to and from hibernacula may lead them to cross roads in great numbers during the fall and the spring (Chan 1993).

In this paper we critically examine the use of road surveys to sample turtles. Many of the potential biases associated with road surveys apply equally to other organisms; therefore, the discussion may prove useful to a wider audience interested in the strengths and limitations to the methodology. Use of road surveys for population has been well described (Campbell and Chrisman 1977). Numerous studies have employed road surveys to obtain information on population structure, relative abundance, or mortality of herpetofauna in Alabama (Dodd 1989), Arizona (Turner et al. 2003), Florida (Duellman and Schwartz 1958; Seigel et al. 2002; Smith and Dodd 2003), Kansas (Busby and Parmalee 1996), Ontario (Ashley and Robinson 1996), and South Carolina (Leiden et al. 1999). Researchers used the technique with various turtles including the Common Snapping Turtle (Chelydra serpentina) (Haxton 2000), Desert Tortoise...
Chrysemys picta Radiated Tortoise (Boarman and Sazaki 1996; Pike et al. 2005), Madagascar Gopher Tortoise (Gopherus polyphemus) (McRae et al. 1981; Boarman and Szaki 1996; Pike et al. 2005), Madagascar

Radiated Tortoise (Geochelone radiata) (Goodman et al. 1994), Painted Turtle (Chrysemys picta) (Whilans and Crossman 1977; Marchand and Litvaitis 2004; Fowle 1996), Striped Mud Turtle (Kinosternon baurii) (Wygodz 1979), and the Texas Tortoise (Gopherus berlandieri) (Bury and Smith 1986; Hellgren et al. 2000). Turtle life history traits and ecology may interact with certain characteristics of roads and seasonal weather patterns to promulgate important biases in the use of this technique. Turtle life history traits and ecology may interact with certain characteristics of roads and seasonal weather patterns to promulgate important biases in the use of this technique.

ASSUMPTIONS OF ROAD SURVEYS

To use road surveys to draw general references about animal populations, the following assumptions must be met: 1) roads should not form a barrier to dispersal; 2) roads should not attract animals; 3) animals should not learn to avoid roads; 4) roads, and associated elements, should not influence species richness or abundance in the immediate area; and 5) individuals should be counted only once per sampling period (Shaffer and Juterbock 1994). Typically, many of these assumptions are violated when road surveys are used to study chelonians.

Roads can form a barrier to turtle dispersal (Gibbs and Shriver 2002; Aresco 2005b). Features like fences, culverts, and retaining walls are often associated with roads and can obstruct the dispersal corridors of many species (Mitchell and Klemens 2000). Researchers should consider the mobility and behavior of the organism in question and consider whether any features associated with roads in their study area might influence the ability of turtles cross (Goodman et al. 1994) and potentially reduce the species' detectability.

The second and third assumptions that roads do not attract or are avoided by animals are important because if either is true, samples from roads will not be representative of the population. Although there is no evidence to suggest that turtles learn to avoid roads, conventional wisdom suggests that individuals that cross roads may be at a selective disadvantage relative to those that avoid roads. If this behavior has a genetic component, vehicular-induced mortality would eventually create a population of turtles with a genetically controlled tendency to avoid roads. This is important for female freshwater turtles whose nesting migration routes are often intersected by roads (Steen and Gibbs 2004), because they tend to show fidelity to nest sites across years (Lindeman 1992). Terrestrial turtles whose home ranges encompass roads are also more vulnerable to mortality relative to those whose home ranges are displaced from vehicle throughways. Under these conditions, one could misinterpret a population’s status when using road counts. The long term effects of this road mortality in turtles are discussed elsewhere (Gibbs and Steen 2005) but may eventually lead to population declines.

There are several characteristics of roads that serve to attract turtles. As poikilotherms, turtles may be attracted to paved roads for thermoregulation. The open canopy above roads coupled with the heat radiating from asphalt (Asaeda and Ca 1993) may provide excellent conditions for basking. This is of particular importance when roads are located in the proximity of wetlands, although heavy traffic volume or extreme temperatures may discourage this behavior. In addition, the soil, vegetation, and thermal properties of roadsides may attract nesting turtles (Seigel 1980; Szerlag and McRobert 2006). Freshwater turtles often nest near ecological edges (Kolbe and Janzen 2002), and may perceive dirt roads and roadsides as suitable nesting habitat. Gopher tortoises, Gopherus polyphemus, often nest in dirt roads (Lora Smith, pers. obs.) which may function as population sinks for turtle populations that demonstrate similar behavior. Egg mortality and increased risk of predation may result due to road maintenance (e.g., Jackson and Walker 1997).

Another assumption, implicit in road surveys, is that features associated with the road itself do not affect species richness or abundance in the vicinity of the road (Shaffer and Juterbock 1994). The vegetation surrounding roads may attract terrestrial turtles due to the increased foraging opportunities relative to other adjacent habitat (Boarman et al. 1997). Roadside ditches may offer habitat to aquatic and semi-aquatic species. For example, Mud Turtles, Kinosternon subrubrum, use roadside ditches as dispersal corridors (David Steen, pers. obs.) and Common Snapping Turtles, Chelydra serpentina, are often found in freshwater drainage culverts on barrier islands (David Steen, pers. obs.).

In contrast, high levels of mortality from collisions with vehicles can substantially decrease local populations of turtles (Gibbs and Shriver 2002) and tortoises (Nicholson 1978; Luckenbach 1982), whereas populations distant from roads are stable. Further, predators of turtle eggs and juvenile turtles, particularly subsidized predators such as raccoons, may be relatively abundant in the edge habitat surrounding roadsides (McDougal 2000), potentially limiting turtle populations (Temple 1987). Ravens, known predators of juvenile tortoises, are drawn to roads (Knight and Kawashima 1993; Boarman and Heinrich 1999). Consequently, roads may have an influence on adjacent turtle populations.

Road surveys are often conducted under the assumption that live individuals are only counted once. Most movements of turtles are not uni-directional (Gibbons 1986), whether they be nesting migrations (Obbard and Brooks 1980), or movements toward a food source or while searching for mates (Stickel 1950). Migrating turtles may risk road mortality two or more times during a single foray as it becomes necessary to repeatedly traverse a road that intersects its route. Female freshwater turtles may make multiple terrestrial movements during the nesting season, potentially resulting in repeated counts of a single individual within a general area. For example, female Pacific Pond Turtles, Actinemys marmorata, have been known to make up to 11 overland nesting migrations within a season (Reese and Welsh 1997), which could, if a road transected this route, lead to one individual being recorded up to 22 times. This potential bias can be remedied by individually marking turtles (Cagle 1939), although processing time should be considered when quantifying sampling effort.

OBSERVATIONAL BIAS

There are several disadvantages intrinsic to road surveys. When driving, even at slow speeds, it is inevitable that some individuals (particularly small or cryptic species) will be misidentified or may escape observation altogether. In many historical road surveys amphibians and reptiles are either absent from species lists or are lumped into broad taxonomic categories (Dickerson 1939; Main and Allen 2002). Such generalizations
could lead to errors in estimates of population parameters. Adult and sub-adult individuals of most turtle species are more often observed on roads than juveniles (Steen et al., unpubl. data), although the reverse may be true in localized areas following emergence of hatchlings from nests (e.g., McCallum 2003). Observations of relatively high numbers of large individuals may be due to the size discrepancy between young and adult animals, but also may be influenced by disparate movement patterns among different size classes (Loughry and McDonough 1996). Additionally, the size of an individual may influence the likelihood that it is scavenged prior to observation (Kimberly M. Andrews, pers. comm.). These observational biases should be noted when discussing turtle communities and species richness determined via road surveys.

**Bias due to the Spatial Ecology of Turtles**

The species observed during road surveys are a reflection of the surrounding habitat, road density, and behavior of that particular species, as well as the skill of the investigator. Habitat specialists may be underrepresented unless a particular habitat is transected by a road. Depending on road density, turtles with small home ranges, highly specific habitat requirements, and limited mobility, (e.g., Bog Turtles, *Glyptemys muhlenbergii*, Chase et al. 1989) are less likely to cross roads than those with large home ranges (e.g., *Gopherus* spp., Diemer 1992). Among freshwater turtles, highly aquatic species, (e.g., Musk Turtles, *Sternotherus* spp.) will be recorded with less regularity than species that frequently undergo terrestrial movements (e.g., *Glyptemys insculpta*).

Furthermore, the sex ratio or age structure of a population may appear biased due to disparities in the movement patterns of aquatic and terrestrial turtles. Within a population, turtles typically exhibit a 1:1 sex ratio (Gibbons 1970; but see Lovich and Gibbons 1990). However, due primarily to their nesting migrations, female freshwater turtles are more likely to be encountered on roads and are often found in greater proportion on roads than in samples based on trapping efforts in wetlands (Steen et al. 2006). The opposite trend is observed among populations of the terrestrial genus *Gopherus* (Steen et al. 2006). Perhaps due to the large home ranges of male tortoises, relative to those of females (Eubanks et al. 2002, 2003), males are more commonly observed along roadways (e.g., McRae et al. 1981) and thus their relative abundance could be easily overestimated within the population.

In addition to seasonality, weather conditions may play a role in how representative a particular sample is of the population as a whole. Freshwater turtles may undertake terrestrial movements, and therefore cross roads, to escape unfavorable habitat conditions related to weather (Gibbons 1986; Aresco 2005b). A road survey conducted during a drought may indicate that a population is increasing relative to previous surveys. However, this may be indicative of individuals undertaking mass migrations to find suitable aquatic habitat (Aresco 2005b), rather than a shift in abundance. Aresco (2005b) found significant differences in the sex ratios and abundances of turtles on roads in drought versus non-drought years and Turner et al. (2003) found annual precipitation may have influenced the species composition of reptiles and amphibians detected in the Whetstone Mountains of Arizona.

**Bias due to Aspects of Roads**

As described, aspects of the natural history of animals may result in sampling bias during road surveys. However, aspects of the roads themselves may also lead to important biases. For example, caution must be exercised when comparing results of road surveys implemented in different geographic areas and on different types of roads. While a turtle may be less likely to approach and cross a high-traffic volume, four-lane highway than a road with less traffic, the highway encompasses more area than a rural two-lane road due to its greater width. Consequently, animals may be observed more readily on these larger roads. When designing studies that aim to compare results from different areas, traffic volume, road type, and width should be considered. The interaction of these factors and their potential influence on wildlife populations is a field that has received little attention.

**Potential Consequences of Road Survey Bias**

The purpose of this section is not to dismiss or reject previous research, but rather to suggest how biases associated with road surveys may influence data collection and interpretation. Aresco (2005b) found populations of freshwater turtles were biased towards males within wetlands in northwestern Florida (Florida Cooter, *Pseudemys floridana*, 80% male; Yellow-bellied Slider, *Trachemys scripta*, 73% male; and Stinkpot, *Sternotherus odoratus*, 65% male). However, turtles intercepted at the roadside exhibited a sex ratio biased towards females (57-72% annual proportion of female turtles). Had only road cruising been employed, an inaccurate estimate of population structure may have been obtained.

Hellgren et al. (2000) employed road surveys while studying the demography of the Texas Tortoise, *Gopherus berlandieri*, but did not specify the percentage of the sample captured with this method. The authors noted juveniles were not as vulnerable to capture with road surveys and were therefore underrepresented. Also, the sex ratio of adults was increasingly male biased with age class; older individuals were more likely to be males. This was attributed to higher male survival rates relative to females, the latter experiencing higher mortality due to complications resulting from calcium deficiencies. However, disparate movement patterns relative to the sex and age of an individual may influence the observed sex ratio on roads. The cumulative average yearly movements of young male Texas Tortoises <150 mm are smaller than those of similar sized females (Auffenberg and Weaver 1969). However, adult males occupy larger home ranges than adult females (Judd and Rose 1983); these individuals may search longer distances for mates, leading to an increased likelihood that they will be encountered on roads than will females of similar age.

Bury and Smith (1986) walked along roads in Texas to detect the same species. They found significantly more male tortoises (n = 67) than females (n = 39) on the roads and in the surrounding vegetation and noted that their results differed from a study conducted ca. 40 km away where 1:1 sex ratios of adults were observed (Judd and Rose 1983). In addition, only 1/107 (0.9%) tortoises captured was a juvenile (Bury and Smith 1986); this differs markedly from the nearby population that contained nearly 25% juveniles (Judd and Rose 1983). While Bury and Smith (1986) walked linear transects along dirt roads to characterize Texas Tortoise populations, Judd and Rose (1983)
searched study plots over a five year period. The varying sex ratios and age structure may be due to biases inherent in linear transects, such as road surveys, as females and juvenile terrestrial turtles are less likely to be encountered with this method. However, differing habitat types between the two sites may have also influenced perceived or actual population parameters.

**CONCLUSIONS AND RECOMMENDATIONS**

There are strategies to minimize potential biases when using road survey data to examine population parameters. Encompassing the entire activity season of a particular species will reduce the influence of seasonal movement patterns. Studies that include road surveys conducted during atypical or varying environmental conditions should identify these events and consider how they may influence observed parameters.

There are clearly biases associated with making inferences about population demography of amphibians and reptiles based on road surveys, and many of these limitations pertain to any type of line transect survey methodology. However, road cruising can still be a useful tool for detecting amphibians and reptiles. By accounting for the inherent limitations of road surveys (Table 1) and employing them in conjunction with various other standardized collecting and trapping techniques, one might obtain a more accurate description of turtle populations. Researchers that incorporate multiple sampling methods should explicitly address the potential biases of each method, and differentiate among data collected using different techniques.

**Literature Cited**


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EVIDENCE OF A NEW NICHE FOR A NORTH AMERICAN SALAMANDER: 
Aneides vagrans RESIDING IN THE CANOPY OF OLD-GROWTH 
REDWOOD FOREST

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Abstract.—We investigated habitat use and movements of the wandering salamander, Aneides vagrans, in an old-growth forest canopy. We conducted a mark-recapture study of salamanders in the crowns of five large redwoods (Sequoia sempervirens) in Prairie Creek Redwoods State Park, California. This represented a first attempt to document the residency and behavior of A. vagrans in a canopy environment. We placed litter bags on 65 fern (Polypodium scouleri) mats, covering 10% of their total surface area in each tree. Also, we set cover boards on one fern mat in each of two trees. We checked cover objects 2–4 times per month during fall and winter seasons. We marked 40 individuals with elastomer tags and recaptured 13. Only one recaptured salamander moved (vertically 7 m) from its original point of capture. We compared habitats associated with salamander captures using correlation analysis and stepwise regression. At the tree-level, the best predictor of salamander abundance was water storage by fern mats. At the fern mat-level, the presence of cover boards accounted for 85% of the variability observed in captures. Population estimates indicated that individual trees had up to 29 salamanders. Large fern mats have high water-holding capacities, which likely enable year-round occupation of the canopy by A. vagrans. Other observations indicate that A. vagrans and its close relative A. ferreus also occupy additional habitats in forest canopies, especially moist cavities inside decaying wood.

Key Words.—Aneides vagrans, A. ferreus, Sequoia sempervirens, forest canopy, arboreal habitat use, salamander

INTRODUCTION

The temperate salamanders of North America are primarily terrestrial and fossorial, except some species in the family Plethodontidae that have been reported to occupy moist vertical rock faces (genus Desmognathus) and several species (genus Aneides) that climb into trees at least seasonally (Petranka 1998; Waldron and Humphries 2005). However, there has been no conclusive evidence of a temperate zone salamander species completing its entire life cycle in an arboreal environment. This report documents the year-round residency of the wandering salamander, Aneides vagrans, in the canopy of old-growth redwood forest in northwestern California.

Recent genetic evidence (Jackman 1998) indicated that the clouded salamander (Aneides ferreus) consisted of two separate species. A new species, the wandering salamander (A. vagrans), was proposed for populations south of the south fork of the Smith River in northwestern California. This species occurs primarily in northern California with disjunct populations that were introduced to Vancouver Island, British Columbia where they are abundant in terrestrial habitats (Jackman 1998; Davis 2002a). The name A. ferreus was retained for populations that occur primarily in western Oregon.

Aneides vagrans has a prehensile tail that it uses to assist in climbing vertical surfaces (Petranka 1998; Spickler and Sillett, pers. obs.) and long limbs with slender digits bearing sub-terminal toe pads (Petranka 1998). This species has previously been described as a primarily terrestrial salamander that is also found on logs, in trees, and on shrubs. It occupies moist terrestrial habitats, especially under exfoliating bark and in cracks and cavities of decomposing logs, stumps, snags, and talus (Davies 2002a; Stebbins 2003). Similarly, A. ferreus has climbing ability with individuals found as high as 6.5 m in trees and, in the laboratory, will leap from the hand to nearby objects, clinging with great tenacity, even to vertical surfaces (Nussbaum et al. 1983). The arboreal salamander (A. lugubris) has been found in trees over 18 m above ground, and may deposit eggs in decay holes in live oak trees up to 9 m above ground (Staub and Wake 2005).

The first evidence that A. vagrans might reside in the temperate forest canopies of the redwood region was the discovery of a clutch of eggs (later hatched in the lab) inside a leatherleaf fern (Polypodium scouleri Hook. & Grev.) mat that had been dislodged from high in the crown of a redwood being felled for lumber (Welsh and Wilson 1995). Soon after the first in situ scientific investigations of old-growth redwood forest canopies began in 1996, we observed the arboreal presence of A. vagrans (Sillett 1999). All observations were made of individuals and pairs occupying tunnels and cavities in large epiphytic fern mats in trees, except one observation (SCS) of a mummified adult found in a shallow trunk cavity located 88 m above the ground in a large redwood tree.

Our objective was to study A. vagrans inhabiting an old-growth forest canopy in Prairie Creek Redwoods State Park, Humboldt County, California, including several trees whose crowns have been explored by two of us (JCS & SCS) since 1996. In particular, we investigated habitat use, activity patterns, and movements in the canopies of five large redwood trees to glean new information on the ecology of A. vagrans in trees.

The Redwood Forest Canopy Environment.—Old-growth forests dominated by Sequoia sempervirens (D. Don) Endl. (hereafter “redwood”) are home to some of the world’s tallest and
largest trees. Individuals can exceed 112 m in height, 7 m in diameter, and have wood volumes over 1,000 m$^3$ (Sawyer et al. 2000). Old-growth redwood forests contain some of the oldest and most structurally complex trees on the planet. These trees often live over 1000 years and develop highly individualized crowns shaped by natural forces (Van Pelt 2001). Disturbances (e.g., windfall, crown fires) that increase light availability within tree crowns stimulate new growth from damaged trunks and branches. In redwood, this new growth can be in the form of either horizontal branches or vertical trunks (hereafter reiterated trunks), each with its own set of branches (Sillett 1999). Reiterated trunks can originate from other trunks or from branches. When a trunk arises from a branch, the branch thickens in response to the added weight and hydraulic demand of the trunk, creating a “limb.” Trunks, limbs, and branches also become fused with each other during crown development (Sillett and Van Pelt 2001). The highly individualized crowns of complex redwoods offer a myriad of substrates and habitats for epiphytic plants and other arboreal organisms (Williams 2006).

Crown-level complexity in redwoods promotes accumulation of organic material, including epiphytic plants, on tree surfaces (Sillett and Bailey 2003). Crotches between the trunks, the upper surfaces of limbs and branches, and the tops of snapped trunks provide platforms for debris accumulation. Vertical and horizontal sections of dead wood also provide substrates for fungal decomposition. Over time, this debris develops into soil as organic materials decompose into humus, which provides a rooting medium for vascular plants. The most abundant vascular epiphyte in redwood rain forests is the evergreen fern, P. scouleri (Sillett 1999), with individual trees supporting up to 742 kg dry mass of these ferns and their associated soils (hereafter ‘fern mats,’ Sillett and Bailey 2003). As fern mats grow in size and number, their effects on within-crown microclimates become pronounced. Like a sponge, large fern mats store water within the crown, increasing the humidity (Ambrose 2004) and providing refuge for desiccation-sensitive species, including mollusks, earthworms, and a wide variety of arthropods (Sillett 1999; Jones 2005). Large fern mats also tend to be internally complex, with tunnels and cavities between the rhizomes and dense roots as well as interstitial space around embedded sticks (Stephen Sillett, pers. obs.).

**MATERIALS AND METHODS**

**Study Area.**—We studied *A. vagrans* in five redwood trees located in Prairie Creek Redwoods State Park (PCRSP), Humboldt County, California within an old-growth redwood forest. Mean annual rainfall in the study area was 1.67 m, with summer temperatures ranging from 7°–31° C and winter temperatures ranging from 1°–23° C during 2002–2004. Trees were selected from a 1-ha permanent reference stand that is 50 m elevation and 7 km from the Pacific Ocean. Within the reference stand, redwood accounts for 95.8% of the trunk basal area with the remainder consisting of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), hemlock (*Tsuga heterophylla* [Raf.] Sarg.), and a few hardwoods.
TABLE 1. Summary of tree size, Polypodium scouleri fern mats, soil water storage, and salamander abundance in five redwood trees from Prairie Creek Redwoods State Park, California. Soil water storage values are whole-tree annual averages derived from a model (Sillett and Van Pelt unpublished). Salamander abundance is the number of Aneides vagrans captured on fern mats in each tree, excluding those captured with cover boards.

<table>
<thead>
<tr>
<th>Tree:</th>
<th>Rhea</th>
<th>Demeter</th>
<th>Kronos</th>
<th>Iluvatar</th>
<th>Prometheus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Height (m)</td>
<td>95.5</td>
<td>97.5</td>
<td>91.6</td>
<td>91.5</td>
<td>97.4</td>
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<tr>
<td>DBH (cm)</td>
<td>405</td>
<td>434</td>
<td>428</td>
<td>614</td>
<td>559</td>
</tr>
<tr>
<td>Main trunk volume (m$^3$)</td>
<td>359.3</td>
<td>389.7</td>
<td>335.4</td>
<td>874.0</td>
<td>598.5</td>
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<td>Reiterated trunk volume (m$^3$)</td>
<td>1.2</td>
<td>20.2</td>
<td>30.5</td>
<td>162.5</td>
<td>63.1</td>
</tr>
<tr>
<td>Limb volume (m$^3$)</td>
<td>1.5</td>
<td>6.4</td>
<td>14.5</td>
<td>24.6</td>
<td>3.2</td>
</tr>
<tr>
<td>Fern mat dry mass (kg)</td>
<td>205</td>
<td>39</td>
<td>275</td>
<td>249</td>
<td>352</td>
</tr>
<tr>
<td>Fern mat dry mass in crotches (kg)</td>
<td>8</td>
<td>6</td>
<td>18</td>
<td>97</td>
<td>249</td>
</tr>
<tr>
<td>Soil water storage (l)</td>
<td>1003</td>
<td>437</td>
<td>1561</td>
<td>1908</td>
<td>4416</td>
</tr>
<tr>
<td>Fern mat salamander abundance</td>
<td>2</td>
<td>3</td>
<td>8</td>
<td>7</td>
<td>14</td>
</tr>
</tbody>
</table>

We selected study trees (Fig. 1) on the basis of size, structural complexity, and epiphyte abundance. Trees 1 (‘Kronos’) and 2 (‘Rhea’) have interdigitating sections of their crowns, where fern-covered branches and limbs allow the possibility of salamander movement from tree-to-tree without going to the ground. Tree 3 (‘Demeter’) stands 16 m from Kronos and Rhea. Its crown does not interact with these trees, so movement of a salamander between them would require ground contact. Trees 4 (‘Prometheus’) and 5 (‘Iluvatar’) stand over 50 m from each other and the other trees; they were selected because of their high crown-level structural complexity and epiphyte loads.

Tree access.—We achieved access to tree crowns by using a high-powered compound bow mounted to an open-face fishing reel. A rubber-tipped arrow trailing fishing filament was shot over branches high in the crown, and a nylon cord was then reeled back over the branches and used to haul a 10 mm diameter static kernmantle climbing rope into the crown and back to the ground. One end of the climbing rope was then anchored at ground level, and the other end was climbed via single rope technique (Moffett and Lowman 1995). We had access to the rest of the crown via arborist-style rope techniques (Jepson 2000; Fig. 2). The climbing rope was threaded through a pulley hung from a sturdy branch near the treetop. The rope could be easily replaced with nylon cord when the tree was not being climbed.

Tree crown mapping.—We described tree crowns by measuring dimensions of the main trunk and all reiterated trunks with a basal diameter over 5 cm. We measured trunk diameters at 5 m height intervals. For reiterated trunks, we recorded: top height, base height, basal diameter, and distance and azimuth (i.e., compass direction) of base and top from center of main trunk. For reiterated trunks, we recorded the following additional measurements: limb basal diameter, diameter of limb at the base of the reiteration, and limb height of origin. Thus, the XYZ coordinates and architectural context of every measured diameter could be determined for use in 3-dimensional mapping. Total tree height was determined by dropping a tape from the uppermost foliage to average ground level.

We derived three structural variables and three fern mat variables from the mapping data, including total fern mat mass (kg), fern mat mass in crotches, proportion of fern mass in crotches, main trunk volume (m$^3$), reiterated trunk volume, and limb volume. Volumes of main trunks, reiterated trunks, and limbs were estimated by applying the equation for a regular conical frustum to the diameter data (Table 1) such as:

Volume = $\frac{1}{3} \times \pi \times (\text{lower radius}^2 + \text{lower radius} \times \text{upper radius} + \text{upper radius}^2)$.

In each tree, we also determined the XYZ coordinates of all Polypodium scouleri fern mats by measuring their heights above ground as well as their distances and azimuths from the main trunk. Fern mat size was quantified by the following measurements: mat length, mat width, average soil depth (calculated from multiple measurements with a metal probe), and maximum frond length. We calculated surface areas of fern mats by applying the equation for an ellipse:

Area = $\pi \times 0.5(\text{mat length}) \times 0.5(\text{mat width})$.

Surface area was multiplied by average soil depth to calculate fern mat volume. Dry masses of all mats were estimated by applying the following model equation ($n = 18$, $R^2 = 0.995$; unpubl. data of Sillett and Van Pelt):

Total mass (kg) = 32.912 × mat volume + 0.0250 × maximum frond length.

To better visualize individual tree crown complexity, we generated three-dimensional models of tree crowns using Microsoft Excel and the crown structure data (Sillett and Van Pelt, unpubl. data). We overlaid locations of fern mats and salamander captures on the crown models via their XYZ coordinates (Fig. 1). We used this information to quantify movements of salamanders captured more than once during the study.

Capturing salamanders.—To locate A. vagrans without destructive sampling, we placed cover objects on fern mats within...
each tree crown. We constructed cover objects from gray fiberglass screening. We cut and folded materials to produce flat envelope-like bags (hereafter ‘litter bags’) that were filled with decomposing leaf litter and soil, producing both small (25 × 20 cm) and large (25 × 40 cm) bags. To limit introduction of foreign materials to the canopy, only litter and soil from each selected site were used to fill the bags.

Placement of litter bags was determined randomly. The total surface area of a tree’s fern mats was calculated by summing the surface areas of all the mats on the tree. Ten percent of the mat area on each tree was covered such that half was covered by each type of litter bag. The probability of an individual fern mat being randomly selected for a given litter bag was proportional to its surface area. Thus, some fern mats, especially large ones, received multiple litter bags while others, especially small ones, received none. The placement of individual litter bags on selected fern mats was not done randomly. Instead, we spaced the bags across the mats in an attempt to minimize the likelihood of their being blown from the crown during storms. This involved nesting the bags into relatively flat regions of the mats. Wooden sticks were placed underneath each litter bag to maintain crawl spaces for salamanders.

Besides litter bags we deployed cover boards, which were crafted from pairs of 2-cm-thick boards cut into 25 × 25 cm sections (Davis 1991). We placed boards together but separated by parallel 1-cm-thick strips of wood that created a crawl space for salamanders. Our cover boards were designed to simulate preferred terrestrial habitats of A. vagrans; 6 mm spaces between bark and heartwood with a smooth firm surface (Davis 1991). This species is often found under the splintered wood of recently fallen trees or exfoliating bark (Davis 2002b; Stebbins 2003). We limited use of cover boards for fear of causing injury to climbers and tourists visiting the grove if the boards happened to fall from the trees. However, we left two cover boards on a large fern mat in Prometheus and one on a large fern mat in Iluvatar. These locations seemed stable enough to prevent loss of the boards during storms. As an extra precaution we equipped the boards with small lengths of cord anchored to the tree.

Access restrictions.—Summer and spring observations were not possible due to climbing restrictions to protect the nesting habitat of two threatened species in the area: the Marbled Murrelet (Brachyramphus marmoratus) and Northern Spotted Owl (Strix occidentalis caurina). Thus, our field season was limited to the fall (late September) through winter (end of January), during three field seasons from 2000 to 2002. During these periods, we checked our cover objects 2–4 times per month, weather permitting. We also made weekly checks of litter bags and cover boards in Prometheus during the 2002-2003 field season, and made one visit to Iluvatar during this time. During each visit, all cover objects were checked. A description of any salamander activity, time and location of each capture were recorded.

Marking salamanders.—We anesthetized captured A. vagrans using a pH neutral solution of MS-222 (3-aminobenzoic acid ethyl ester) achieved by combining 1.0 g MS-222 + 2.4 g sodium bicarbonate dissolved in 500 ml distilled water. Once salamanders were immobile, they were permanently and uniquely marked under anesthesia with 1 x 2 mm fluorescent alphanumeric tags (Northwest Marine Technologies, Inc., Seattle, Washington, USA) injected subcutaneously on the ventral side of the tail immediately posterior to the vent. Photographs of dorsal patterns were taken of salamanders too small to be injected with tags. Marked animals were returned to their point of capture once fully recovered from the MS 222. We recorded snout to vent length (i.e., from tip of snout to anterior margin of vent), total length, number of costal folds between adpressed limbs, weight (to the nearest 0.1 g), sex if recognizable by secondary sexual characteristics (e.g., shape of head, presence of mental glands, cirri, eggs in oviducts), and any injuries or other identifying marks.

Data analyses.—We used stepwise multiple regression analysis to evaluate potential effects of individual fern mat characteristics on salamander abundance in those mats with cover objects (n = 65). The following independent variables were included: percentage of surface covered by litter bags, total area covered by litter bags, total surface area, dry mass, and height above ground. The number of cover boards on each fern mat (0, 1, or 2) was also used as an independent variable to account for the potential effects of this sampling technique. The dependent variable was the number of salamander captures per mat.

We evaluated potential effects of fern mats and tree structure on A. vagrans abundance using correlation analysis. Tree-level independent variables (n = 5) included total fern mat mass (kg), mass of fern mats in crotches, and the average amount of water stored (l) in each tree’s fern mats throughout the year. This last variable was derived from a canopy soil hydrology model developed for the permanent reference stand that includes all of the trees in this study (Sillett and Van Pelt, unpubl. data). Structure variables included volumes (m$^3$) of each tree’s main trunk, reiterated trunks, and limbs. The dependent variable was the number of marked animals per tree. We corrected for sampling effort by dividing the actual number of visitations per tree (n = 27–33) by the highest number of visitations for any tree. We eliminated the potentially confounding effects of cover boards by removing those two mats from the data set prior to the analysis.

Tree-level salamander abundance was estimated with the Chapman (1951) method (see Chao and Huggins 2005). We used the unbiased estimator for population size ($N$):

$$N = \frac{(M + 1)(C + 1)}{R + 1} - 1$$

where $M =$ number of individuals marked in the first sample, $C =$ total number of individuals captured in the second sample, and $R =$ number of marked individuals recaptured in the second sample. For this analysis, we made the following assumptions: 1) sampling was random; 2) the population was closed (i.e., no immigration, emigration, birth, or death) within each field season; 3) all animals had the same chance of being caught in the first sample; 4) marking individuals did not affect their catchability; 5) animals did not emigrate, birth, or death, and $C =$ total number of individuals captured in the second sample.
not lose marks between sampling intervals; and 6) all marks were reported on discovery in the second sample. We recognize that there are limitations to this method (see Pollack et al. 1990) but our small samples did not permit a more sophisticated approach. As a consequence we consider these estimations only as first approximations of salamander abundance in fern mats.

**Other salamander observations.**—The inaccessibility of study trees during the spring and summer greatly limited our ability to make year-around observations of arboreal *A. vagrans* activity. However, several relevant observations were made by forest activists participating in "tree-sits" at other nearby locations, and by scientists working in the canopy on research unrelated to this study. We include a summary of these anecdotal observations with our results because these accounts fill gaps in our temporal record and provide documentation of salamander presence in the canopy throughout the entire year.

**RESULTS**

**Tree-level population estimates.**—A total of 55 captures were made of 42 individual *A. vagrans*, including 13 recaptures. One individual was captured five times, two individuals were captured four times, three individuals were captured twice, and 36 individuals were captured only once. Captured individuals ranged from 1.3–7.1 cm in SVL, 2.4–14.7 cm in total length, and 0.1–5.9 g in mass. Salamanders were found in all five study trees with the most captures in Prometheus (n = 28) and the least in Rhea (n = 2). Small sample sizes forced us to use entire field seasons as sampling intervals to make population estimates for each tree. Thus, *A. vagrans* abundance was estimated once for three trees (Prometheus, Iluvatar, Kronos) in January 2002 for animals marked in the first field season and recaptured in the second field season (8–11 individuals per tree), and again for two trees (Prometheus and Iluvatar) in January 2003 for animals marked in the second field season and marked or recaptured in the third field season (20–29 individuals per tree, Table 2). There were insufficient data to make any tree-level population estimates for two of the trees (Demeter and Rhea). However, we combined data from all five trees to calculate an estimate of 54 salamanders for these five tree crowns collectively in January 2002 based on animals marked in the first field season and marked or recaptured in the second field season (Table 2).

**Tree-level effects on salamander abundance.**—Based on correlation analyses at the tree-level, there were two significant predictors of salamander abundance per tree: average water storage by fern mats ($r = 0.930$, $P = 0.022$) and mass of fern mats in crotches ($r = 0.885$, $P = 0.046$). Our small sample size (n = 5 trees) prohibited further analyses of tree-level effects for other fern mat variables (total fern mat mass, proportion of total fern mass in crotches), and three structural variables (main trunk volume, reiterated trunk volume, and limb volume).

**Effects of fern mat characteristics on salamander captures.**—Fern mat-level effects on *A. vagrans* captures and recaptures were evaluated separately for a total of 65 fern mats (i.e., only those with cover objects) in five trees using regression analysis. Total number of *A. vagrans* captured, including recaptures, was positively associated with number of cover boards ($R^2 = 0.38$, $P < 0.0001$), area covered by litter bags ($R^2 = 0.28$, $P < 0.0001$), fern mat mass ($R^2 = 0.22$, $P < 0.0001$). No associations were found between captures and either the percentage of fern mat surface area covered by litter bags ($R^2 = 0.002$, $P = 0.70$) or height ($R^2 = 0.004$, $P = 0.62$). Stepwise multiple regression analysis revealed that number of cover boards (adjusted $R^2 = 0.85$, $P < 0.00001$), fern mat mass (cumulative $R^2 = 0.90$, $P < 0.00001$), and height of fern mat (cumulative $R^2 = 0.91$, $P < 0.03$) all accounted for significant amounts of variation in the number of salamander captures.

The strongest variable affecting the number of *A. vagrans* captured was not a physical characteristic of the fern mats, but was an artifact of our sampling technique. Significantly more salamanders were captured on fern mats with cover boards than on mats with only litter bags. In Prometheus, the total number of captures on one fern mat was 15, representing 5 individuals. All of the captures were made in two cover boards, although 8 litter bags occurred in close proximity to the cover boards. Nine of the 15 captures were recaptures, including four of a single large male who apparently took up residence in an area that included both of the cover boards, which were located < 0.5 m apart. He was captured during all 3 years of the study, and on several occasions he was found with other salamanders. On one fern mat in Iluvatar, there were 9 captures representing seven individuals. Seven of these were made in a cover board, while the remaining two were made under a litter bag located 75 cm away.

**Movement of recaptured salamanders.**—We found no evidence of among-tree movements of marked salamanders, via interacting crowns or the ground. Of the 13 recaptures, 12 were of individuals found in the same locations as their initial captures. The single exception was a juvenile *A. vagrans* (1.2 g, SVL= 4.35 cm) found under a litter bag (first capture) and then recaptured a week later on the surface of a fern mat 7.5 m higher in the tree.

**Seasonal activity.**—Our limited field season precluded observations of seasonal differences in movement and habitat use, but based on our findings and several anecdotal observations made outside of our field seasons (see below), it appears that at least some individual *A. vagrans* occupy the forest canopy throughout the year.

**Other observations.**—The few spring and summer observations were often made while canopy researchers were conducting surveys for protected species (Marbled Murrelet and Spotted Owl). Also, salamander observations were made by non-scientists illegally occupying trees to protect them from logging. It is understandable that the protection of threatened species takes priority over new research dealing with a salamander that appears to be abundant, at least in terrestrial habitats, but the lack of data for these seasons left us with several unknowns concerning the life history and ecology of *A. vagrans* in redwood forests. The following observations may help us to understand *A. vagrans* behavior during these periods.

The willingness of tree sitters to stay aloft for extended periods enables them to make observations that scientists working under research permits cannot afford to do. In the spring of 2002, an activist designated as Remedy began a tree-sit on private timber lands. Remedy, along with other activists, established sleeping platforms in several large redwoods near Freshwater, in coastal...
Humboldt County, California. Remedy remained aloft for nearly a year before being forcibly removed and arrested for trespassing. In that time period she made numerous observations of a pair of wandering salamanders.

On seven occasions from April to September, Remedy observed the “same pair” of wandering salamanders moving within an area around a small cavity located 3 m from her living platform. The original leader of the tree had broken at an approximate height of 40 m; the living platform was located a few meters below the break. The loss of the leader occurred at least 100 years before, and two reiterated trunks had replaced it. A zone of decaying wood had formed around the break created the cavity that the salamanders occupied. The same cavity was also shared by a small “tree squirrel,” probably a Douglas’ Tree Squirrel (Tamiasciurus douglasi) or a Northern Flying Squirrel (Glaucomys sabrinus). A P. scouleri fern mat occupied the top of the broken trunk.

Remedy often observed the salamanders moving in close proximity to each other, but they appeared to be “moving independently as if unaware of each other.” Most of the salamander activity was limited to the area on and around the fern mat, but on two occasions a salamander moved out along branches and continued to the outer crown where it could no longer be seen. All observations were made during early evening and under similar microclimatic conditions: dry substrate with elevated air humidity. Conditions were described as “warm and muggy, perfect weather for flying insects.” One stated impression was that the salamanders were more affected by temperature than by moisture as no animals were observed moving during the rain or immediately thereafter. There was limited flying insect activity during and immediately after rain storms. Observations were always made during calm conditions with high air humidity and low cloud cover; the tree’s microclimate was “merely damp.”

Remedy reported an A. vagrans eating while in the canopy. One evening, she noted an insect, a “winged termite,” alight on a small branch approximately 30 cm from the salamander. The salamander then rapidly moved to the insect, which it ate without hesitation. After a moment, the salamander continued moving along the branch to the outer crown.

Similar observations were made by another activist, Raven, participating in a tree-sit in the Van Duzen watershed in Humboldt County. Raven made several observations of a pair of A. vagrans foraging near his sleeping platform. He also described how A. vagrans activity decreased along with decreasing nighttime temperatures as autumn and winter approached. On 2 February 2003, he observed a pair of A. vagrans move on to his platform. He watched them for several minutes before they continued off into the darkness.

On 17 September 2002 at 0800 hrs, one of us (Stephen Sillett) and his graduate student (A. Ambrose) observed an adult A. vagrans while crown-mapping a large redwood in Humboldt Redwoods State Park. The observation was made during warm conditions with high air humidity and low cloud cover; the tree’s bark was dry. We observed a single adult A. vagrans moving vertically along the trunk at a height of 93 m above ground. The salamander’s path was exposed with no soil or obvious cover nearby. The nearest area of apparent cover was in a cavity of dead wood located 100.6 m above the ground, but the surface of this site was also exposed and dry. Obvious fissures and crevices in the decaying wood, however, likely allow such animals to enter and retire within damp cavities.

We also have made incidental observations of A. ferreus, a close relative of A. vagrans. On three separate occasions in 2002, one of us (James Spickler) and N. Bowman observed adult A. ferreus while studying the nesting behavior of the red-tree vole (Arborimus pomo) in old-growth Douglas-fir forests of coastal Oregon (BLM forest lands, Salem and Eugene Districts). Observations were made in the summer (July-August), midday during periods with high humidity and on moist substrates. In all cases, salamanders were inactive and hidden within the stick nests of a western grey squirrel (Sciurus griseus). Two of these salamanders were found in an active nest containing fresh feces and elevated temperatures from the recently departed rodent’s body.

In 1993, Stephen Sillett observed an A. ferreus while conducting canopy research in a 700-year-old Douglas-fir forest (Middle Santiam Wilderness Area, Willamette National Forest, Willamette Oregon; see Sillett 1995). While climbing in a large Douglas-fir tree adjacent to a 30-year-old clearcut, he found an adult salamander under moss (Antitrichia curtipendula) on a large branch approximately 30 m above the ground. After being disturbed, the salamander moved horizontally across the branch and retreated under a bark flake on the tree trunk. The observation was made midday during the dry season (early autumn), and the moss mat was “merely damp.”

**DISCUSSION**

Plethodontid salamanders are unique in that they are the only salamander family to have invaded the tropics, where many species occupy arboreal niches (Lynch and Wake 1996). However, in spite of the high number of species displaying arboreal habits in tropical forests, little is known about this phenomenon beyond a few anecdotal accounts (e.g., Good and Wake 1993; McCrannie and Wilson 1993). Our results here provide information on a new niche dimension for a North American temperate zone plethodontid salamander, the resident use of arboreal habitats in redwood forest canopies by Aneides vagrans.

Like other plethodontid salamanders, A. vagrans is lungless and respires exclusively through its skin and buccopharynx. Presumably, this requires the maintenance of skin moisture to facilitate respiratory gas exchange (Shoemaker et al. 1992). The skin of most amphibians is highly permeable to liquid and gas, allowing for moisture exchange rates similar to those of standing water (Spotila and Berman 1976). To avoid fatal desiccation, amphibians have developed a variety of behavioral and physiological means by which to control water loss (Shoemaker et al. 1992). Plethodontid salamanders select habitats with suitable microsites that retain relatively high moisture contents as the macrosite begins to dry (Thorson 1955; Cunningham 1969; Ovaska 1988; Cree 1989; Shoemaker et al. 1992). This desiccation-avoidance behavior has been observed in terrestrial A. vagrans (Davis 2002b).

Our correlation analysis of tree-level effects on salamander abundance highlights the importance of water storage in soils beneath epiphytes and location of this material within the crown (e.g., in crotches). Soils on limbs drain faster than those in crotches (Ambrose 2004; Enloe et al. 2006) and thus may become too dry for perennial occupancy by salamanders. Microclimate data from fern mats show that crotches have more stable moisture and temperature regimes than branches or limbs (Ambrose 2004;
Although the arboreal feeding habits of A. vagrans, enabling this salamander to breed and potentially live its entire life within tree crowns.

The effects of fern mat size and height on salamander captures are ecologically interpretable. The positive correlation between fern mat size and A. vagrans abundance can be attributed to the larger surface area available for foraging, higher water-holding capacity, and greater internal complexity of larger fern mats. Although the arboreal feeding habits of A. vagrans have not been studied, the salamanders probably take prey from fern mats. Fern mat surfaces (at least seasonally) have more invertebrate biomass than other surfaces (e.g., bark and foliage) in redwood crowns (Jones 2005). In fact, the mites and collemboles inhabiting fern mats experience population explosions during the wet season, and have densities similar to those observed in terrestrial habitats under similar conditions (Jones 2005).

Larger, deeper fern mats have greater water storage and slower rates of desiccation than smaller mats (Ambrose 2004), thus providing more stable, moist microclimates conducive to A. vagrans habitation. As a fern mat increases in size, new roots and rhizomes grow to replace the old ones, which subsequently decay. Although debris from litter fall, especially tree foliage, is a major component of the P. scouleri fern mats, the majority of organic material in these mats comes from P. scouleri itself, especially humus derived from decaying roots and rhizomes (Sillett and Bailey 2003). Dead, decomposing rhizomes leave behind “tunnels” in the soil. Larger debris (e.g., branches) that falls onto fern mats can also create tunnels and internal cavities as it is covered by other debris and begins to decompose. On three occasions, Sillett and Bailey (2003) found A. vagrans occupying interstitial spaces in P. scouleri mats (mats were being harvested for the development of equations to predict fern mass). Also, an egg cluster of A. vagrans was found within a P. scouleri mat on a freshly fallen old-growth redwood (Welsh and Wilson 1995). These observations suggest that the tunnels and cavities in fern mats are used by A. vagrans, and it is likely that they are important refugia, but the fragile nature of the substrate makes searching the tunnels nearly impossible without permanently altering the habitat.

The negative effect of fern mat height on salamander captures can be attributed to the varying microclimates at different heights within a forest canopy. During periods with no precipitation, the upper canopy receives more light and wind, and the air is less humid compared to the lower canopy (Parkery 1995, Sillett and Van Pelt, unpubl. data). Therefore, fern mats in the upper canopy, regardless of size, are subjected to more frequent and severe periods of desiccation than those in the lower canopy. In redwood forest canopies this effect can be seen in P. scouleri itself. Although fern mat size is not correlated with height, the size and shape of fronds become progressively smaller with increasing height in the forest (Sillett and Bailey 2003). The negative effect of height on number of A. vagrans captured can be attributed to the less stable microclimate of upper canopy fern mats compared to those in the lower canopy. Fern mats higher in a tree may be important for salamanders foraging during wet periods, but the prolonged occupation of these sites may be risky during dry periods. This idea is supported by our discovery of two mummified individuals near the tops of two trees over 90 m tall (see also Maiorana 1977).

Dead wood may represent another important habitat for arboreal salamanders in redwood forests. At the forest level, the average water storage in dead wood (16,500 l ha⁻¹) rivals the amount stored in canopy soil (19,700 l ha⁻¹), and seasonal variation in dead wood water storage is less than that in soils on branches and limbs (Sillett and Van Pelt, unpubl. data). Even though we did not quantify salamander abundance in dead wood habitats, a number of anecdotal observations suggest that A. vagrans use dead wood and hollow cavities. The highest observation of this species ever made (93 m) was of a salamander climbing upwards on a late summer morning towards the dead, broken top of a large redwood nearly lacking vascular epiphytes and soil. It is likely that large populations of A. vagrans reside within hollow trunks of standing redwoods in old-growth forests.

Movement and territoriality.—If a salamander finds a habitat that has a favorable moisture regime and sufficient prey availability, it would be advantageous for the animal to stay in that habitat or return to it frequently (Jaeger 1980). Terrestrial A. vagrans move only short distances, are site-tenacious, and return periodically to particular habitats within their home range (Davis 2002a). Our canopy findings parallel these terrestrial observations.

On 6 occasions we captured more than one salamander on a fern mat. Twice we found two males in a cover board with a single female. We also found two females together with no male present and two males together with no female present. Twice we found a pair of salamanders on the same fern mat but not within the same cover board: a male with a female and a male with another male. Males did not appear to be defending females from other males, and neither sex appeared to be defending a particular site, both of which are major components of territorial behavior (Brown and Orians 1970; Jaeger et al. 1982; Mathis et al. 1995). Similar behaviors were observed in terrestrial A. vagrans on Vancouver Island, British Columbia (Davis 2002a). Although arboreal A. vagrans in redwood forests appear to be acting similarly to terrestrial individuals in British Columbia, we did not sample during either the breeding season (presumably spring) or the summer. Arboreal A. vagrans may behave differently during certain times of the year if resources, such as nest sites, prey items, or moist habitats, become limited.

Seasonality.—The seasonal restrictions on canopy research in old-growth redwood forests prevented us from sampling salamanders for eight months of the year, including the summer dry season. When considering the hydric constraints of plethodontid salamanders, it is likely that A. vagrans would be less active on forest canopy surfaces during the dry season. Anecdotal observations of A. vagrans, as well as observations of other species of Aneides, suggest otherwise however. Arboreal Aneides may be most active during the drier and warmer spring and summer given the strong marine influences that contribute to mild temperatures and high relative humidity during these seasons in the coastal redwood forest (Sawyer et al. 2000).
Green salamanders \((Aneides aeneus)\) use arboreal habitats seasonally (Waldron and Humphries 2005). These animals overwinter in rock outcrops and migrate into woody or arboreal habitats (primarily hardwoods) during the onset of spring. They remain in these habitats throughout the summer and breeding season before returning to rock outcrops sometime in October and November. Green Salamanders prefer larger (in diameter) and more complex trees having a variety of visible cavities. On dry days individuals are often found under the flaky and furrowed bark of several different tree species. The maximum height above the ground where Green Salamanders have been observed is 21 m at the mouth of a tree hollow (Waldron and Humphries 2005). Gordon (1952) noted a decrease in Green Salamander abundance during the dry season, but Waldron and Humphries (2005) demonstrated that the salamanders may be climbing into the canopy where they remain throughout the summer and cannot be easily detected from the ground.

It is unlikely that \(A.\ vagrans\) utilizes arboreal habitats seasonally like \(A.\ aeneus\). Anecdotal observations do not support such a scenario but instead suggest year-round residency. At most, \(A.\ vagrans\) may shift its use of particular microhabitats within the canopy, but it remains unclear which suitably moist locations might be preferred during different seasons.

**Effects of tree- and fern mat-level variables on salamanders.**—Our mat-level analysis indicated an effect of cover boards on number of salamanders. Nearly half of the \(A.\ vagrans\) captured during our study were found in cover boards even though their use was quite limited. By placing cover boards on top of fern mats we may have created a preferred habitat type. This assertion is supported by observations that dead wood substrates were favored by terrestrial \(A.\ vagrans\) populations in Vancouver Island, British Columbia (Davis 2002b). It is unclear whether the salamanders captured in our cover boards were residents of the fern mat on which the boards were placed, originally residing in the tunnels and other complexities of the fern mat, or if placing the cover boards on the fern mat created a habitat allowing foraging individuals from other parts of the tree the opportunity to stay and take up residence. The paucity of recaptures under litter bags suggests that \(A.\ vagrans\) prefers crevices but will use litter bags opportunistically for cover while foraging.

**Future research.**—Future studies should examine how \(A.\ vagrans\) uses other habitats besides fern mats, since the preponderance of cover board captures as well as anecdotal observations suggest that \(A.\ vagrans\) inhabits crevices, cavities, and lodged woody debris at least as much as it does soil beneath ferns (\(P.\ scouleri\)). Crevices and cavities are difficult to search manually in a non-destructive fashion, and we discourage this activity. Placing cover boards adjacent to these sites would allow capture of salamanders coming out to forage on other tree surfaces without permanently altering the habitat. Cover boards also create new habitats within tree crowns for salamanders and their prey. The entrance to natural and artificial crevices and cavities could be monitored continuously (even during summer months when canopy access is restricted) via motion-sensitive, infrared video cameras. Microclimate data could also be compared to videos to determine preferred conditions for foraging and also to document salamander behavior throughout the annual cycle. Identification of salamanders via videos would be possible using a visual implant fluorescent elastomer marking technique and by marking individuals on their dorsal surfaces.

Hopefully our discovery of resident arboreality in \(Aneides vagrans\) will trigger a renewed interest in studying adaptations of plethodontid salamanders to the use of arboreal habitats. For example, the recently described modification (Sapp 2002) of the typical plethodontid courtship tail-straddling walk (Houck and Arnold 2003) from linear to circular in the genus \(Aneides\) may be an adaptation to arboreality.

**Conservation implications.**—Resident populations of arboreal salamanders in old-growth forests may be top predators of diverse, heterotrophic communities fueled by the productivity of epiphytes and the trees themselves. Such ecosystems appear to be lacking in younger forests regenerating on logged-over land. Only 4% of the original old-growth redwood forests remain, and second-growth forests originating before 1930 are scarce (Noss 2000). Nearly all regenerating redwood forests are younger than rotation age (~50 years) and consisting of trees less than 40 m tall with small branches. As a consequence of their simple structure, the biological diversity of young redwood forests is low, and many old-growth-associated plants and animals are now restricted to a few National and State Parks (Sawyer et al. 2000; Cooperrider et al. 2000). Redwood forests capable of supporting arboreal salamanders are rare outside of these Parks. Even within the Parks, epiphytic vascular plants and associated soil communities do not occur in the crowns of small trees despite their proximity to large trees, because the structural complexity (e.g., large limbs and reiterated trunks) necessary to support these organisms develops very slowly. Thus, the arboreality of \(A.\ vagrans\) in redwood forests may be a phenomenon restricted to a tiny portion of the landscape. Further investigations to establish a basis for the conservation of \(A.\ vagrans\) and associated organisms in protected forests are warranted.

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SExual Differences in the Ecology and Habitat Selection of Western Toads (Bufo boreas) in Northeastern Oregon

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Abstract.—Several species of toads (family Bufonidae), including the Western Toad (Bufo boreas) have declined in the western United States. Information on toad ecology and habitat use is essential to determine potential causes for population declines, as is the potential relationship between this information and disturbance events. Aspects of western toad survival, mortality, movements, habitat selection, and diet were investigated at five study areas in northeastern Oregon during summers of 2002-2005. Of 100 radio-tagged toads monitored for one summer during these years, 32% survived until September, 29% were killed by predators, 10% died of other causes, and 29% were missing or had lost transmitters. At four study areas sampled in 2005, 24% of 37 males and 44% of 32 females sampled during the breeding season, and three dead male toads found after the breeding season tested positive for Batrachochytrium dendrobatidis. Females traveled significantly farther than males, and the maximum distances traveled by female and male toads were 6230 m and 3870 m, respectively. Toads with transmitters selected habitats: (1) with little or no canopy; (2) on south-facing slopes; (3) near water; and (4) with high densities of potential refugia (e.g., burrows, rocks, logs). Males were more closely associated with water than females. Twenty-six toads overwintered in rodent burrows (38%), under large rocks (27%), under logs or root wads (19%), and under banks adjacent to streams or a lake (15%). Diet consisted of 82% ants (Formicidae), 13% beetles (Coleoptera), and <1% in 8 additional orders of insects with no differences detected between male and female toads. Disturbance events, such as wildfire, can influence refugia and prey of toads, and climatic conditions may influence a toad’s susceptibility to B. dendrobatidis.

Key Words.—Bufo boreas; diet; habitat selection; movements; northeastern Oregon; predation; Western Toad.

INTRODUCTION

The decline of many amphibians is causing concern worldwide and reasons for the declines are often unknown (Carey 1993). Populations of the Western Toad (Bufo boreas) have declined in many parts of their range including in the central Rocky Mountains (Carey 1993; Corn et al. 1997; Livo and Yeakley 1997), California Great Central Valley (Fisher and Shaffer 1996), northern Utah (Corn et al. 1997; Thompson et al. 2003), and the northern Great Basin (Wente et al. 2005). Due to their declining populations, numbers of the Western Toad have been listed as: (1) endangered by New Mexico and Colorado; (2) Native Species Status 1 by the Wyoming Game and Fish Department; (3) a “Sensitive Species” by the U.S. Forest Service; and (4) a candidate species for federal listing under the Endangered Species Act (Loeffler 2001; Jones et al. 2005).

Some toad declines have been associated with fungal and bacterial infections. In Colorado, declines in Western Toads were attributed to Batrachochytrium dendrobatidis (B.d.) (Daszak et al. 1999; Green and Muths 2005; Scherer et al. 2005) and the bacteria Aeromonas hydrophila (Carey 1993). Other species of toads in the West have shown declines as well, with chytridiomycosis linked with die-offs of the Yosemite toad (B. canorus), Wyoming Toads (B. hemiphris Baxteri), and B. californicus (Kagarise Sherman and Morton 1993; Carey et al. 1999; Daszak et al. 1999; Green and Kagarise Sherman 2001; Carey et al. 2003; Muths et al. 2003). The fungus (Saprolegnia ferax) may have been responsible for egg mortality in a population of Western Toads in Oregon (Blaustein et al. 1994).

Disturbance events, such as fire and insect outbreaks, may affect Western Toads by impacting water quality and solar radiation, abundance of prey and predators, habitat quality in movement corridors, and terrestrial summer and winter refugia. Deliberate habitat alterations, such as fuel reductions, may cause toads to be more vulnerable to predation, starvation, disease, or desiccation during movements to these habitats. Little information is available on how disturbance events influence Western Toads in the northwest, although some information is available for other areas. For example, more B. americanus were trapped in burned than in unburned deciduous forests in Appalachian Mountains of eastern North American (Kirkland et al. 1996). Boreal Toads bred in shallow ponds in burned stands of Lodgepole Pine (Pines contorta) in Glacier National Park and not in adjacent unburned areas (Pilieod et al. 2006).

Due to the population declines of Western Toads elsewhere, one objective of this study was to establish baseline data on demographics of populations in northeastern Oregon. Although this research is exploratory in nature, I am testing the hypotheses that female and male Western Toads do not differ in survival, mortality, movements, habitat use, and diet during the post-breeding period.

MATERIALS AND METHODS

Study areas.—Toads (n = 472 females and 1297 males) were monitored from 2002 to 2005 at five areas on the Wallowa-Whitman National Forest in Baker, Wallowa, and Grant Counties in northeastern Oregon. Toads were monitored and radio-tagged at breeding sites in May or June at Fish Lake (Fish; 1992 m elevation), Twin Lake (Twin; 1944 m), Lilypad Lake (Lilypad; 2130 m), Crawfish Lake (Crawfish; 2094 m), and Balm Reservoir (Balm; 1368 m). The two reservoirs (Balm and Fish) are each
about 35 ha in size and are used for crop irrigation 13-18 km downstream in the summer. Approximately 80% of the water was removed from each reservoir in August and September each year during our study. Lilypad, Crawfish, and Twin are lakes that range from 2.5 ha to 7.3 ha in size and whose water levels fluctuated by < 0.5 m during this study. All five bodies of water contained Rainbow (Oncorhynhus mykiss) or Brook Trout (Salvelinus fontinalis). Breeding sites were typically in shallow water on south-facing shores at four of the study areas, but were on the south-, east-, and north-facing shores at Balm. One breeding site was used at Crawfish, two at Twin, three at Lilypad, four at Fish, and six at Balm. Breeding sites with egg strings separated by >100 m were considered to be separate sites.

All study areas were in mountainous, forested terrain with undulating uplands and moderately or steeply walled drainages. Forests consisted primarily of Lodgepole Pine and Subalpine Fir (Abies lasiocarpa) at all study areas except Balm Reservoir, where Ponderosa Pine (Pinus ponderosa), Douglas-fir (Pseudotsuga menziesii), Western Larch (Larix occidentalis) and Grand Fir (A. grandis) were present. Stand replacement fires (i.e., crown fire that kills the overstory trees) burned portions of the forests surrounding Fish, Twin and Crawfish between August 1994 and 1996. The burned stands were not logged and had high densities of standing dead trees and downed wood. Streams, springs, and seeps were common in all the study areas except Balm.

Daytime ambient temperatures in summer typically exceeded 24°C, and winter low temperatures were typically freezing with an extreme of -15°C in the study areas. Annual precipitation averaged 78 cm with about 60% falling as snow, depending on the elevation. At Fish and Twin, snow was on the ground from October until June each year with maximum depths of 3-6 m. At the other study areas, snow was on the ground from November until May with maximum depths of 1-3 m.

Study areas were selected based on the presence of at least 20 Western Toads at breeding sites and accessibility by vehicles during breeding activity. There were few water bodies to select from because high densities of Western Toads are uncommon in high elevation lakes in northeastern Oregon (Bull and Marx 2002). High densities of Western Toads have not been reported elsewhere in the Blue and Wallowa Mountains.

Population demography and telemetry.—To assess population dynamics, toads were captured with dip nets at breeding sites between early May and mid-June. I inserted a passive integrated transponder (PIT) tag for individual identification (Loeffler 2001), determined sex, snout-vent length (SVL) [measured to the nearest mm], and mass (to nearest g) for each toad. A toe was removed from a front limb of the smallest and largest male and female toad during breeding at each study area in 2005 to determine age using skeletochronology. Swab samples were taken from a limited number of toads in 2005 to test for the presence of B.d. Toad populations were monitored at Crawfish, Lilypad, and Balm each spring from 2003 to 2005 and at Fish in 2002, 2004, and 2005. Toads were monitored at Twin in 2002, but the breeding site was inaccessible during the other years.

One hundred toads were also radio-tagged (models BD-2G and BD2, Holohil Systems Ltd., Carp, Ontario, Canada) at the five study areas. Radio-tagged toads were monitored in Fish and Twin in 2002, Crawfish and Lilypad in 2003, and Balm in 2003-04. Transmitters weighed 1.8 g, performed for 5 months, and had a range of 50-500 m depending on the disposition of the toad (above or below ground). Transmitters were attached to males and females without eggs with a 3-mm wide satin ribbon fitted around the waist or with a thin satin ribbon (2 mm) around the upper arm for toads with narrow hips or gravid females (in 2002 only) (Bull 2000). Ribbons were both glued and stitched to the transmitter with carpet thread through the tunnel that was embedded in the acrylic at the anterior end of the transmitters.

An alternative temporary attachment technique using absorbable suture material was developed for: (1) gravid females; (2) toads that developed abrasions from the sativan ribbon around the waist or arm; and (3) all toads still carrying transmitters in September each year. This attachment did not restrict oviposition, allowed abrasions to heal, and, importantly, allowed the transmitter to fall off when the sutures dissolved. This was critical for toads with radios on into the winter because waistbands can cause serious injury (cuts > 0.5 cm deep, pers. obs.) if not removed. These transmitters were attached by stitching the transmitter to the dorsal surface of the toad, adjacent to and on either side of the spinal column between the shoulder blades and urostyle, with absorbable suture material (i.e., polydioxanone monofilament synthetic absorbable suture; size: 3/0 and 2/0). The suture material was sewn through the skin only of the toad either with a sewing needle or by putting a 20 gauge hollow needle (2.5 cm long) through the skin of the toad and passing the suture material through the needle. A horizontal stitch 8-10 mm in length was used and the suture material was knotted with three square knots to provide a good anchor for the transmitter. One person could attach the transmitter without sedating the toad in less than 10 minutes. It is unknown if this transmitter attachment technique affected the behavior and movements of the toads.

Radio-tagged toads were located with a portable receiver (Telonics TR-4, Mesa, Arizona, USA) and H-type directional antenna each week from capture until the transmitter failed or came off, the toad was preyed upon or died, the signal could not be detected, or until late November when snow and cold conditions inhibited toad movement. Toads were located between 0900 and 1700, and the location was confirmed visually 49% of the time. During this study, toads were typically in refugia during the day, so the time of day that each toad was located was not randomized.

In order to estimate longevity and age at sexual maturity, age estimates were determined using skeletochronology (Matson’s Laboratory LLC, Milltown, Montana USA); the lines of arrested growth in transverse sections taken from the mid-diaphysis phalanges of arbitrarily selected toads were counted (Guarino et al. 1995). The relationship between estimated age, SVL, and mass for females and males was determined using Pearson’s correlation coefficient.

Survival, mortality, and chytridiomycosis.—The fate of toads was classified as alive, preyed upon, dead with no evidence of predation, missing, transmitter off, or other. When only the transmitter and band were found on the ground, it was unknown if the toad had been killed by a predator or if the transmitter had come off. If the tunnel was broken on the transmitter or there were tooth marks, it was attributed to predation because it is unlikely the toad would be strong enough to break the tunnel in the acrylic. Toads located in the same underground burrow for a month were excavated to determine their condition.

Predation was attributed to avian species when the transmitter was in a tree or the toad remains were accompanied by white excrement. Avian or mammalian predators were assigned responsibility when remains included the bones of the head and portions of the back, only the skin turned inside out, or the legs of the toad had been consumed with the skin turned inside out (Olson 1989; Corn 1993; Kagarise Sherman and Morton 1993).

When a signal could not be detected, the toad was classified as...
Habitat use and availability.—To assess these aspects of toad ecology, habitat characteristics of the location where radio-tagged toads were found were recorded each week in 2002 and 2003. Each time a toad was located, I determined its habitat (in water or terrestrial location) and recorded the type of shelter used (i.e., none, self-excavated depression, burrow, rock, log, root wad, bark, or stump). Outside of the breeding season, toads were typically underground or under cover during the day and were not disturbed. Landscape characteristics were recorded visually in approximately 1-ha circular area around the toad. The presence of an opening (area without woody vegetation) at least 15 m in diameter within 10 m of the toad was noted. Vegetation type was classified as open forest (< 30% canopy closure), closed forest (30% canopy closure or more), riparian, burn, scab flat, or rock slope. Structural stage was classified as no trees, stems initiation, stem exclusion, young multi-stage, or old multi-stage (Oliver and Larson 1990). Harvest activity (Balm only) was classified as open forest (< 30% canopy closure), closed forest (≥ 30% canopy closure or more), riparian, burn, scab flat, or rock slope. Activity was classified as none, partial cut, or clear-cut. Fire activity was classified as none, understory burn, or overstory burn. Slope gradient and aspect were recorded, as well as the distance to water, green forest, and/or burned forest, if applicable.

Micro-habitat characteristics were recorded in a 0.005-ha circular plot (4-m radius) with the toad as the center point. Canopy closure (using GRS densitometer) was determined by averaging five readings at plot center and 1 m away in four cardinal directions. The number of live and dead stems < 20 cm and 20 cm dbh (diameter at breast height) and larger were counted. Ground cover was estimated as the percent of bare ground, water, rock, forbs, shrubs, grass, and logs in each plot. The number of burrows and shelters that were large enough to accommodate a toad (an opening ≥ 5 cm in diameter) were counted in each plot.

Twenty-six over-wintering sites were identified in October and November when toads ceased moving and snow covered the ground. Habitat characteristics were recorded as described for summer habitat. The depth of toads in burrows underground was measured with a rigid tape measure and flashlight. Toads in over-wintering sites in fall 2003 and 2004 were located again in December and January to verify that they had not made any additional moves since the previous location in November.

To assess potential habitat selection by toads, available terrestrial habitat was measured in the five study areas at randomly selected points within a calculated radius of each breeding site. The radius of the circle that contained the random points was determined by taking the mean of the farthest distance each radio-tagged toad traveled from the breeding site in each study area. I used the mean rather than the maximum distance because the greatest distance was traveled by large females, and it was unknown if the smaller males were capable of traveling this distance. Only toads monitored for at least 7 weeks were included in calculating the mean. The maximum dispersal distance and number of random points were determined at the end of September during the year toads were monitored. Available habitat was assessed at Fish and Twin in September 2002 and at Balm, Crawfish, and Lilypad in July 2004. Conditions of most habitat variables measured did not change appreciably between July and September except ground cover. I recorded percent ground cover by vegetation type because the plant species composition would be consistent over time even though the height of grasses, forbs, and shrubs would likely change. The number of random points approximately equaled the number of toad locations during 2002-03 at terrestrial sites in each study area. I generated random points with a uniform distribution within the circle using ArcView (ESRI Inc., Redlands, California, USA) and the Animal Movement version 1.1. extension for ArcView (Hooge, P.N., and B. Eichenlaub. 1997. Alaska Biological Science Center, United States Geological Survey, Anchorage, Alaska, USA.).

Available habitats and habitat at toad locations were compared using a multivariate analysis of variance (MANOVA) for continuous variables (percent slope; percent canopy closure; distance to a burned forest, green forest, and water; number of stems < 20 cm and ≥ 20 cm dbh; percent ground cover) and Mann-Whitney U tests for categorical variables (slope aspect, vegetation type, structural stage, presence of an opening, harvest activity, fire activity, number of burrows, and shelters). If MANOVA results were significant, separate ANOVAs were used to examine individual habitat variables. The number of burrows and shelters were treated as categorical variables because these variables are skewed to low numbers and are not normally distributed. Only toad locations at terrestrial sites were used for comparisons with available habitat. The same statistical comparisons were used to determine if habitat use differed by sex.

Diet.—An adequate source of prey may reflect the quality of habitat, so diet samples were collected from radio-tagged toads each week to determine what they ingested. Diet samples were obtained in all study areas where toads were accessible from 21 May through 24 September 2002 and 2003, which corresponds to
the time that toads are active (pers. obs.). Diet samples were also collected opportunistically when toads without radios were encountered.

A diet sample was obtained by stomach flushing with a plastic flexible catheter (2 mm wide, 56 cm long) inserted through the mouth and esophagus of the toad with the opposite end attached to a 65-cc syringe filled with water (Legler and Sullivan 1979; Whitaker et al. 1983). Stomach flushing is expected to have limited adverse impact on the population, and it allows resampling of the same individual. The use of stomach flushing (rather than dissection) may introduce bias toward smaller size classes, with larger items becoming stuck in the esophagus, although palpating the stomach after flushing reduced this bias. Diet samples were preserved in vials of 75% ethanol and returned to the lab for identification. After the diet sample was removed by flushing, the stomach was palpated to ensure that the stomach was empty. After stomach flushing, crickets (Gryllus sp.) were fed to each toad to replace the sample taken. Prey items were identified at least to order, and placed in body-length size classes (1-4.5, 5-9.5, 10-14.5, and 15 mm and larger; Bull 2003). Biomass (in mg) was determined after oven-drying each sample for 24 h at 40°C. Prey types and availability at these locations are unknown.

Dietary composition was defined as the percentage of items of a particular prey type out of the total number of prey items. The diet composition, number and size of prey items, and biomass were compared by month (three time periods: May-June, July, August-September), study area, and sex using a MANOVA. Diet composition was compared for orders, families, and genera that comprised > 5% of the prey items. Pearson’s correlation coefficient was used to assess correlation between biomass and number of prey items. Probability levels of < 0.05 were considered significant for all statistical comparisons.

**RESULTS**

**Population demographics.**—A total of 1,769 toads were PIT-tagged between 2002 and 2005. The highest number of toads and the highest ratio of females to males occurred at Balm (Table 1). Data on mature toads captured at each breeding site are shown in Table 1. Of 14 female toads I aged using skeletochronology, the youngest and oldest at a breeding site were 1.9 and 10.8 years, respectively. Of 20 male toads, the youngest and oldest at a breeding site were 1.9 and 7.7 years, respectively. There was a correlation in male toads between age and SVL (r = 0.47, P = 0.04) and between age and body mass (r = 0.52, P = 0.02); there was no correlation in females between age and these variables. Females lost 20-44% of their body weight after depositing eggs (n = 5).

The recapture rate (percentage of toads recaptured in successive or alternate years) was 2-37% and varied by study area (Table 1). During 2003-2005, two females were gravid in consecutive years at Balm.

**Survival.**—Of 100 radio-tagged toads in five study areas, 32% survived until September of the year they were monitored, at least 30% were preyed upon, and chytridiomycosis was the likely cause of death in at least 6% (Table 2). Fifteen of 46 females (33%) and 31% of 54 males survived until September. Only the transmitter was recovered in 13 cases; thus it was not possible to verify if the toad had been consumed by a predator. It was unlikely that transmitters slipped off, although not impossible. The fate of an additional 16 toads was unknown because their signals could not be detected, and their radios were not recovered.

**Predation.**—At least 26% of radio-tagged males and 33% of females were killed by predators. Of the 13 males killed, 38% were killed at the breeding site, while only 25% of the 16 females

<table>
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<tr>
<th>Characteristic</th>
<th>Balm</th>
<th>Twin</th>
<th>Fish</th>
<th>Crawfish</th>
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<td></td>
<td></td>
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</tr>
<tr>
<td>SVL</td>
<td>104(73-126)</td>
<td>119(115-123)</td>
<td>102(86-130)</td>
<td>101(95-107)</td>
<td>93(91-96)</td>
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<tr>
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<td>130(120-141)</td>
<td>105(56-185)</td>
<td>102(94-110)</td>
<td>71(60-79)</td>
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<td>3</td>
<td>4</td>
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<tr>
<td>SVL</td>
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<td>90(69-110)</td>
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<td>Female:male ratio</td>
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<td>-</td>
<td>3%*</td>
<td>-</td>
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<tr>
<td>Males</td>
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<td>34%</td>
<td>12%</td>
<td>37%</td>
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<td>Distance (m) traveled</td>
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<td>2067(260-3560)</td>
<td>1670</td>
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<td>7</td>
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<td>0</td>
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<tr>
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<td>1248(390-2180)</td>
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<td>4</td>
<td>6</td>
<td>3</td>
<td>6</td>
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</tbody>
</table>

*Represents two females that were gravid in two consecutive years, and two females that were gravid in 2003 and in 2005.
*Represents one female that was gravid in 2002 and in 2005.
were killed at the breeding site; all others were killed away from
the breeding site. The highest predation rate (37% of tagged
toads) occurred at Balm Reservoir where avian species were
presumed responsible for at least 74% of the predation (Table 2).
I was unable to distinguish between avian and mammalian
predation at Lilypad Lake and Fish Lake. No predation was
detected at Crawfish and Twin.

Eight radio-tagged and 21 unmarked toads were found skinned
along the shore of Balm Reservoir in 2004. These deaths were
attributed to raven predation based on observations of ravens,
presence of white excrement, and the absence of mammal tracks.
Six transmitters were found in trees at Balm Reservoir. Two
transmitters were located in an active Red-tailed Hawk (Buteo
jamaicensis) nest, three were in trees about 100, 250, and 450 m
from the nest, and I observed a red-tailed hawk capture a toad at
the shoreline and carry it to the nest. Therefore, the six
transmitters found in trees in 2004 were attributed to red-tailed
hawk predation. Osprey (Pandion haliaetus) also frequented the
reservoir and could have been responsible for some of the
transmitters in trees. Two radio-tagged toads were found in
Common Garter Snakes (Thamnophis sirtalis). The predator of 7
toads could not be determined conclusively. In these cases, only
a small piece of the toad remained with the transmitter or the
transmitter was found with a broken tunnel.

**Batrachochytrium dendrobatidis.**—In 2005, 24% of 37 tested
males and 44% of 32 tested females returned positive results for
B.d. at the four study sites sampled. A higher incidence of B.d.
was detected in females than in males at three of four study sites.
Advanced B.d. infection was found in three male toads found dead
at terrestrial sites at Balm Reservoir 1-3 weeks after leaving the
breeding site, and a mild chytrid infection was detected in one live
toad at Lilypad Lake (U.S. Geological Survey 2004). Mortality
due to chytridiomycosis may have been underestimated given that
an additional five dead radio-tagged toads showed no evidence of
predation but tissue samples submitted for histology determination
of infection were too desiccated to determine fungal infection

**Movements.**—The majority of Western Toads in these study
areas left the breeding ponds and traveled in a relatively straight
line from the breeding site to an area where they remained for
the rest of the summer (Fig. 1, 2); only toads monitored for at least 7
weeks are included in this section on movements. SVL and mass
of male and female toads were not significantly correlated with the
distance each toad traveled. The maximum distance traveled by a
toad was 6230 m. Females traveled significantly farther (mean =
2543 m, SE = 267.9, n = 27) than males (mean = 997 m, SE =
151.4, n = 28) from the breeding sites for those toads monitored at
least 7 weeks (t = -5.07, df = 53, P < 0.01; Table 1). Twenty-four

![Figure 1](image-url)
of 27 females moved more than 1600 m from the breeding site, and three females moved only 180, 260, and 930 m away. Only 8 of 28 males monitored at least 7 weeks traveled more than 1000 m from the breeding site. Toads in Balm tended to travel the farthest distances, although sample sizes were inadequate to compare among study areas (Table 1).

Females typically left the breeding site 1 or 2 days after egg laying, while males remained at the breeding site for 1 to 4 weeks and often traveled between different breeding sites at the pond or lake. The number of days for toads to reach summer habitat largely depended on the distance traveled per day, but the rate of movement (m/day) to the summer habitat was not statistically different between males and females. The slowest rate of travel for male and female toads was 17 m/day and the fastest was 241 m/day. The shortest number of days to reach summer habitat was 16 days (1080 m movement at 67.5 m/day), and the longest was 83 days (5400 m movement at 66.1 m/day). Some toads crossed rugged terrain to reach summer habitat; two females traveled 2.4 km down steep cliffs to the Imnaha River which was 530 m lower in elevation. Two toads climbed 200 m in elevation up rock
TABLE 2. Fates of 100 radio-tagged Western Toads (percentage of toads) monitored between the breeding season (May or June) and 1 September of 1 year (2002, 2003, or 2004).

<table>
<thead>
<tr>
<th>STUDY AREA</th>
<th>Balm</th>
<th>Twin</th>
<th>Fish</th>
<th>Crawfish</th>
<th>Lilypad</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alive</td>
<td>16%</td>
<td>83%</td>
<td>79%</td>
<td>20%</td>
<td>38%</td>
<td>32%</td>
</tr>
<tr>
<td>Total predation</td>
<td>37%</td>
<td>0%</td>
<td>21%</td>
<td>0</td>
<td>23%</td>
<td>29%</td>
</tr>
<tr>
<td>Avian/mammalian</td>
<td>33%</td>
<td>0%</td>
<td>21%</td>
<td>0</td>
<td>23%</td>
<td>27%</td>
</tr>
<tr>
<td>Snake</td>
<td>3%</td>
<td>0%</td>
<td>0%</td>
<td>0</td>
<td>0%</td>
<td>2%</td>
</tr>
<tr>
<td>Radio off or redation*</td>
<td>16%</td>
<td>0%</td>
<td>0%</td>
<td>40%</td>
<td>8%</td>
<td>13%</td>
</tr>
<tr>
<td>Dead, not predation*</td>
<td>11%</td>
<td>17%</td>
<td>0%</td>
<td>0</td>
<td>0%</td>
<td>8%</td>
</tr>
<tr>
<td>Missing‡</td>
<td>16%</td>
<td>0%</td>
<td>0%</td>
<td>40%</td>
<td>31%</td>
<td>16%</td>
</tr>
<tr>
<td>Other‡</td>
<td>3%</td>
<td>0%</td>
<td>0%</td>
<td>0</td>
<td>0%</td>
<td>2%</td>
</tr>
<tr>
<td>No. radio-tagged toads</td>
<td>62</td>
<td>6</td>
<td>14</td>
<td>5</td>
<td>13</td>
<td>100</td>
</tr>
</tbody>
</table>

*Toads may have slipped their transmitters or been consumed by a predator.
*Three of these toads were confirmed as having died of B. dendrobatidis and another five were too desiccated to determine fungal infection.
‡Missing toads could have moved out of the range of detection or been carried off by a predator or the transmitter may have quit from mechanical problems.
†One toad was run over on a gravel road, and one toad died after it became entangled in vegetation.

Habitat selection.—After breeding, toads were primarily terrestrial (81% of the locations on land, 19% in the water away from breeding sites). Of the terrestrial locations, 81% of the toads were in refugia and 19% were on the surface. Refugia used by toads included: rocks (31%); burrows (18%) (Fig. 3); logs (17%); self-excavated depressions (8%); and stumps, root wads, or bark (6%).

In all five study areas combined, toads used vegetation types, burn activities, harvest activities, and percent slope in proportion to their occurrence (162 toad locations at Fish, 66 at Twin, 113 at Lilypad, 129 at Balm, 57 at Crawfish). In the three study areas where a portion had been burned by wildfires in the last 10 years, 56% of the toad locations and 58% of the random plots were in burned forests. Toads did not use certain habitat characteristics at random ($F = 46.64, df = 975, P < 0.01$; Table 3). In all study areas, toads selected south-facing slopes and avoided north-facing slopes compared to random plots (Table 3). Areas with no trees and seedlings were used more and older stands used less than expected based on availability ($Z = -2.63, P < 0.001$). Toads occurred in openings > 15 m in diameter 62% of the time and in forests 38%, yet only 39% of the random plots occurred in openings and 61% in forests ($Z = -7.33, P < 0.01$). In the 4-m radius plots, toads typically selected locations that had more open forest canopy and were closer to burrows used for refugia than occurred at random plots (Table 3). The ground cover at toad locations had more rocks (Fig. 4), more water, more forbs, fewer logs, and less bare ground compared to random plots (Table 3). Toad locations were also closer to water compared to random plots; the type of water at toad locations included streams (69%), permanent standing water (22%; e.g., ponds, springs), and temporary water (9%).

Differences in the use of habitat between sexes were observed ($F = 6.81, df = 481, P < 0.01$) with males more closely associated with water. Twenty-six percent of radio-tagged males were at aquatic locations, whereas only 5% of the locations of radio-tagged females were aquatic. Overall, locations of radio-tagged males were significantly closer to water ($F = 8.42, P < 0.01$), had a higher percentage of water in the 4-m radius plots ($F = 19.38, P < 0.01$), and were farther from burrows ($F = 4.31, P = 0.04$) than locations of radio-tagged females. More locations of radio-tagged females were found: (1) in openings ($Z = -3.91, P < 0.01$); (2) on south and west slopes ($Z = -3.01, P < 0.01$); and (3) at locations with more open canopy ($F = 11.97, P < 0.01$), fewer trees < 20 cm dbh. ($F = 4.31, P = 0.04$), more bare ground ($F = 19.51, P < 0.01$), more forb cover ($F = 9.81, P < 0.01$), and less shrub cover ($F = 5.48, P = 0.02$) compared to males. These observations suggest that females selected sites that received more solar radiation.

The mean distance of hibernacula from breeding sites was 1968 m (range = 180-6230 m, $N = 26$). Toads arrived at over-wintering areas between 16 September and 10 November. Toad movements were monitored until October or late November depending on the study area, although snow covered the ground in all areas before we terminated monitoring. I found that some toads moved up to 2 m underground or between locations even in November after snow covered the ground. No movements among hibernacula were detected between late December and January with 1-2 cm of snow on the ground ($n = 5$, Balm and Lilypad).

FIGURE 3. Western Toads ($Bufo boreas$) frequently used rodent burrows for thermoregulation and protection from predators.
TABLE 3. Mean values of micro-habitat variables recorded at locations of 100 radio-tagged Western Toads after toads left the breeding sites in five study areas, 2002-2003. An overall multivariate analysis of variance reflected significant differences between habitat at 527 toad locations and 501 random plots. Number in parentheses is the standard error.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Toad</th>
<th>Random</th>
<th>F value</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Canopy closure (%)</td>
<td>25 (1.25)</td>
<td>42 (1.50)</td>
<td>65.34</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Distance to water (m)</td>
<td>46 (3.70)</td>
<td>133 (5.79)</td>
<td>154.24</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Distance to burrow (cm)</td>
<td>29 (4.57)</td>
<td>372 (28.07)</td>
<td>146.32</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Distance to green forest (m)</td>
<td>68 (6.74)</td>
<td>92 (10.6)</td>
<td>3.88</td>
<td>0.05</td>
</tr>
<tr>
<td>Stems &lt; 20 cm dsh</td>
<td>5.4 (0.42)</td>
<td>8.4 (0.54)</td>
<td>22.47</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Stems ≥ 20 cm dsh</td>
<td>0.5 (0.04)</td>
<td>1.5 (0.8)</td>
<td>128.66</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Ground cover (%)</td>
<td>23 (0.92)</td>
<td>32 (2.86)</td>
<td>7.83</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Grass</td>
<td>16 (0.73)</td>
<td>16 (0.78)</td>
<td>0.59</td>
<td>0.44</td>
</tr>
<tr>
<td>Forbs</td>
<td>20 (0.68)</td>
<td>15 (0.64)</td>
<td>16.18</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Shrub</td>
<td>12 (1.00)</td>
<td>12 (0.76)</td>
<td>0.52</td>
<td>0.47</td>
</tr>
<tr>
<td>Rock</td>
<td>18 (0.98)</td>
<td>15 (0.94)</td>
<td>8.30</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Log</td>
<td>9 (0.48)</td>
<td>12 (0.44)</td>
<td>12.39</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Water</td>
<td>7 (0.52)</td>
<td>3 (0.25)</td>
<td>7.59</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Slope aspect (%)</td>
<td></td>
<td></td>
<td>Z = -3.59</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>North</td>
<td>19%</td>
<td>32%</td>
<td></td>
<td></td>
</tr>
<tr>
<td>East</td>
<td>31%</td>
<td>26%</td>
<td></td>
<td></td>
</tr>
<tr>
<td>South</td>
<td>33%</td>
<td>22%</td>
<td></td>
<td></td>
</tr>
<tr>
<td>West</td>
<td>17%</td>
<td>20%</td>
<td></td>
<td></td>
</tr>
<tr>
<td>No. burrows in 4-m radius</td>
<td>1.6 (0.13)</td>
<td>0.9 (0.09)</td>
<td>Z = -7.14</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>No. shelters in 4-m radius</td>
<td>3.5 (0.27)</td>
<td>1.9 (0.16)</td>
<td>Z = -7.97</td>
<td>&lt;0.01</td>
</tr>
</tbody>
</table>

Toads over-wintered underground in rodent burrows and under large rocks, logs or root wads, and banks adjacent to streams or a lake (Table 4). Standing water or streams were observed within 1 m of the hibernacula at 7 of 26 over-wintering sites. Six of the 10 over-wintering sites in burrows had been excavated by Red Squirrels (Tamiasciurus hudsonicus) based on the presence of middens and cone scales at the burrows. The remaining four over-wintering sites in burrows were likely excavated by red squirrels or ground squirrels (Spermophilus spp.). None of the toads were known to hibernate communally.

Diet.—In 2002 and 2003, 91 diet samples were collected at the five study areas (N = 33 males and 16 females). One sample was collected from each of 27 toads, 2 or 3 samples from each of 19 toads, and 4-7 samples from each of 3 toads over a 4 month period. More than 90% of the samples were collected from toads captured on land versus in water. The mean size of sampled toads was 104 (SE = 2.7) mm SVL and 99 g mass (SE = 5.9) for females and 89 (SE = 1.3) mm SVL and 63 g mass (SE = 2.8) for males. The mean number of prey items per sample was 20.3 (SE = 3.1, range of 1 to 228) with a total of 1844 prey items identified (Table 5). There were no significant differences between sexes, among time periods, or among study areas in the number or size of prey items, diet composition, or total flushed biomass.

Prey items found in diet samples indicate that the Western Toad consumes primarily ants and ground beetles at these study areas with no differences between the sexes. Toads concentrated on terrestrial arthropods that were < 15 mm in size and seemed to take advantage of arthropods that were ground-dwelling and colonial. Very few aerial or aquatic arthropods were found in the diet samples. Toads appeared to use areas with a high density of ants but were also opportunistic and ate passing invertebrates within the size range that they could handle. More prey items (mean = 30.5, SE = 8.50, n = 31) were found in diet samples collected in burned forests compared in green forests (mean = 15.0, SE = 1.55, n = 60), although these were not statistically different (t = 1.79, df = 32, P = 0.08).

Ants (Formicidae) (82%) and beetles (Coleoptera) (13%) represented 95% of the prey items identified in the samples (Table 5). Eight additional orders of insects and two classes of arthropods each comprised < 1% of the diet, and arachnids comprised 2.2% of the samples. Twelve individual prey items were larval forms, and six of these might have been aquatic forms. Of the prey items that could be measured, 24% were 1-4.5 mm in body length, 47% were 5-9.5 mm, 26% were 10-14.5, and 3% were 15 mm or larger. Mean biomass of diet samples was 12.5 (SE = 1.6) mg with a range of 0.1 to 79.4 mg. Biomass of the diet sample was correlated with number of prey items (r = 0.66, P < 0.01), which suggests that toads foraged on many small prey items versus a few large ones.

DISCUSSION

Population demographics.—Large declines in the numbers of Western Toads at these breeding sites were not detected during this study. I marked the most toads at the two reservoirs (1105 individuals at Balm and 593 at Fish) in spite of these sites experiencing high fluctuations in water levels compared to the three lakes with constant water levels. Differences between males and females were detected in predation rate, presence of B.d., movements, and habitat use during this study. No differences were detected in diet and overall survival between females (33%) and males (31%). The behavioral differences in movements and habitat use between the sexes likely influenced their vulnerability to predation. Too little is known regarding the transmission and effects of B. dendrobatidis on the Western Toad in these study areas to determine how their behavior influences this mortality factor or how B.d. influences behavior in Western Toads.

Females had a higher rate of mortality overall, but predation at the breeding sites was higher for males probably because males spend more time at the breeding sites than females. Most predation occurred during the post-breeding period at terrestrial locations. Numerous other studies have documented predators of adult Western Toads, although only Olson (1989) and Corn (1993) calculated a predation rate of > 60% and > 20% at breeding aggregations in Oregon and Colorado, respectively.

More females than males tested positive for B.d. through PCR at Fish, Crawfish, and Balm; no toads were tested at Twin and only one male was tested (positive) at Lilpad. The only dead animals found that tested positive for B.d. via PCR analysis were radio-tagged males from Balm. It is unknown if B.d. causes mortality at the other study areas, although Balm, at the lowest elevation, has the warmest and driest conditions of the five study areas which may have influenced the toad’s susceptibility to the fungus (Carey et al. 1993). The effect of climate on B.d. in amphibians is unclear although temperature and precipitation have...
been implicated in the infection with and impact of B.d. on amphibians (Daszak et al. 2003; Woodhams and Alford 2005; Pounds et al. 2006). Carey et al. (2006) reported that air temperature between 12°C and 23°C had no significant effect on survival time of B. boreas toadlets infected with B.d. Additional research is needed to determine the extent of mortality caused by B.d. in Western Toads and the influence of local weather.

**Movements.**—Telemetry enabled me to monitor movements of individual toads for an entire active season. Although the majority of the movement data was collected using waistbands on toads, the benefits of the alternative temporary transmitter attachment outweighed the difficulties. Stitching transmitters to toads with dissolvable suture material allowed me to monitor toad movements to hibernacula where the transmitters eventually fell off with no apparent lasting harm to the toads. I recaptured 5 toads 6 months or 1.5 years after they went into hibernation with transmitters sewn through the skin and could detect no obvious injury (pers. obs.).

Sixty-seven percent of 27 females moved > 2000 m from the breeding site while only 14% of the males moved > 2000 m. Potential reasons for these “long distance” movements include reducing the risk of predation, finding food sources, reducing competition for prey, colonization of other breeding sites, or finding warmer microclimates to allow activity later in the season. The period of activity at high elevation study areas was slightly over 3 months; finding a location with any thermal advantage and abundant prey to extend the active season would be presumably advantageous. Another factor that likely facilitates “long distance” travel may be water availability. The use of streams as travel routes has been documented in western Montana (Adams et al. 2005). The longer distances traveled by females may be related to their larger size and greater capacity to store and carry water in their lymph sacs and bladder (Bartelt et al. 2004).

Males that traveled a short distance (< 500 m) in the summer or moved back toward the breeding site in the fall, as occurred at Fish, Crawfish and Lilypad, could easily return to the breeding site in the spring. These three study areas were also the ones with the highest recapture rate of male toads. In contrast, toads that over-winter more than 2000 m from the breeding site may be unable to return in time to breed the next spring. Breeding occurs within days after the ice melts on the lakes, and in spring snow and freezing temperatures are likely to impede movement and extend travel time. The distances toads traveled from the breeding sites in this study exceeded the distances reported in other studies. In southeastern Idaho, male toads traveled an average of 581 m and females a mean of 1105 m from the breeding site (Bartelt et al. 2004). In Colorado, Muths (2003) reported the maximum distance traveled from the breeding pond in one season was 2324 m for a female and 972 m for a male. Also in Colorado, two female toads traveled maximum distances of 5756 m and 6485 m during a summer (Carey et al. 2005). The ratio of female to male mean maximum distances traveled was 2.4

Table 5. Number of prey items identified to order, family, or genus found in 91 Western Toad diet samples in northeastern Oregon, 2002-2003. Numbers of diet samples with each prey item are listed. Families with fewer than three representatives are not listed separately. Percent of prey items are listed by order only.

<table>
<thead>
<tr>
<th>Class/Order/Family</th>
<th>Prey items (N)</th>
<th>Samples with prey item (N)</th>
<th>% by order</th>
</tr>
</thead>
<tbody>
<tr>
<td>Insecta</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hymenoptera (ants, bees, and wasps)</td>
<td>91</td>
<td>83</td>
<td>81.9</td>
</tr>
<tr>
<td>Formicidae (ants)</td>
<td>439</td>
<td>45</td>
<td></td>
</tr>
<tr>
<td>Formica (Formica ants)</td>
<td>625</td>
<td>48</td>
<td></td>
</tr>
<tr>
<td>Camponotus (carpenter ants)</td>
<td>429</td>
<td>49</td>
<td></td>
</tr>
<tr>
<td>Vespidae (wasps)</td>
<td>7</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>Coleoptera (beetles)</td>
<td>57</td>
<td>12.6</td>
<td></td>
</tr>
<tr>
<td>Carabidae (ground beetles)</td>
<td>67</td>
<td>23</td>
<td></td>
</tr>
<tr>
<td>Staphylinidae (rove beetles)</td>
<td>23</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>Curculionidae (snout beetles)</td>
<td>13</td>
<td>11</td>
<td></td>
</tr>
<tr>
<td>Scarabaeidae (scarab beetles)</td>
<td>6</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Orthoptera (grasshoppers)</td>
<td>124</td>
<td>39</td>
<td></td>
</tr>
<tr>
<td>Lepidoptera (butterflies and moths)</td>
<td>16</td>
<td>10</td>
<td>0.9</td>
</tr>
<tr>
<td>Heteroptera (true bugs) (&gt;1 families)</td>
<td>8</td>
<td>6</td>
<td>0.4</td>
</tr>
<tr>
<td>Trichoptera (caddisflies)</td>
<td>6</td>
<td>4</td>
<td>0.3</td>
</tr>
<tr>
<td>Odonata (dragonflies)</td>
<td>5</td>
<td>1</td>
<td>0.3</td>
</tr>
<tr>
<td>Homoptera (hoppers, aphids)</td>
<td>1</td>
<td>1</td>
<td>0.1</td>
</tr>
<tr>
<td>Plecoptera (stoneflies)</td>
<td>1</td>
<td>1</td>
<td>0.1</td>
</tr>
<tr>
<td>Arachnida (arachnids)</td>
<td>30</td>
<td>2.2</td>
<td></td>
</tr>
<tr>
<td>Araneae (spiders)</td>
<td>25</td>
<td>23</td>
<td></td>
</tr>
<tr>
<td>Opiliones (harvestmen)</td>
<td>11</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td>Acari (mites and ticks)</td>
<td>5</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Diplura (centipedes)</td>
<td>4</td>
<td>3</td>
<td>0.2</td>
</tr>
<tr>
<td>Diplopoda (millipedes)</td>
<td>3</td>
<td>1</td>
<td>0.2</td>
</tr>
</tbody>
</table>
Habitat selection.—Habitat that allows behavioral thermoregulation, water absorption, prey, over-wintering sites, and protection from predators is essential for toad survival. Toads appeared to be seeking habitat that included areas: (1) with open forest canopies or openings in the landscape with no trees; (2) with south-facing slopes; (3) close to water; and (4) with a high density of burrows, rocks, or logs that could be used for cover. The difference in habitat conditions selected by sexes suggested that water was more important to males, perhaps because of their smaller size and less capacity to store water (Bartelt et al. 2004). The selection of more open locations enabled toads to maintain a higher body temperature, which likely facilitated growth if ground dwelling prey were available (Lilywhite et al. 1973; Bartelt et al. 2004). These conditions are likely advantageous for replenishing body reserves after laying hibernacula (Loeffler 2001) cited unpublished data that indicated boreal toads hibernated below the frost line in ground squirrel burrows, which was similar to 38% of the hibernacula I detected (Table 4). In California, Western Toads remained underground in gopher or ground squirrel holes during the day and throughout the freezing part of the night in March at 2025 m elevation (Mullally 1952). The portions of the hibernacula that were accessible to me were damp and likely did not freeze due to deep snow cover and their depth underground (Bull and Carter 1996).

Diet.—Diet samples suggest that Western Toads consume primarily ants and ground beetles at these study areas with no difference between the sexes. The tendency of toads to be underground during the day resulted in a limited number of diet samples; however, the sample size in this study is larger than other studies reporting diet, most of which involved dissections of toad stomachs (Burger and Bragg 1947; Campbell 1970b; Miller 1978). Three other studies reported the same predominance of ants that we detected. In Colorado, toads ate mostly ants, beetles, and spiders, although representatives from 43 invertebrate families were found in 33 stomachs (Campbell 1970b). Miller (1978) found 75% Hymenoptera, 23% Coleoptera, 3% Arachnida, and <1% Diptera, Lepidoptera, Orthoptera, and Diplopoda in seven toad stomachs in Montana. Moths, grasshoppers, ants, deer flies, mosquitoes and beetles (Staphylinidae, Dytiscidae) were found in 15 toad stomachs in Colorado (Burger and Bragg 1947).
fires (that were not logged) were used by toads in proportion to their occurrence. In addition, toads traveled shorter distances in burned forests than in green forests. This observation suggests that suitable habitat conditions and food were found closer to the breeding site than in green forests or that travel is considerably more hazardous. Changes in vegetation following wildfires could influence toads through thermoregulation and water conservation, predation, and prey or burrow availability.

Fuel reductions are being implemented across the western United States to reduce the risk and severity of wildfires. Fuel reductions are designed to reduce the amount of coarse woody debris in treated stands (Bull et al. 2005) and may impact toads negatively in areas where logs and other woody material are used for refugia. Removing large amounts of woody debris, clear-cutting or other harvest activities may greatly limit toad movements and habitat use, particularly during dry weather (Bartelt et al. 2004). The removal of coarse woody debris from the forest floor also reduces the amount of nesting substrate for some species of Camponotus and Formica ants (Torgersen and Bull 1995), which are prey for the Western Toad. Additionally, the effects of these fuel reduction treatments on squirrel species (that create burrows used by toads) and on populations of ants and ground beetles (prey for Western Toads) are unknown. Research is needed to determine if the changes in vegetation following wildfires in different habitats are beneficial or detrimental to toads.

Large declines in numbers of breeding toads were not detected over the course of this study even though B.d. was present in all study areas. The study area where three male toads died with B.d. infections severe enough to have caused mortality, also had the lowest recapture rate of males (3%). Additional research is needed to determine if this low recapture rate of male toads is due to mortality by B.d. or other causes. Predation in some of the study areas may be high enough to cause declines over time, depending on the rate of recruitment at these sites. It is unclear whether the risk of predation associated with breeding sites may be responsible for the extensive movements I detected or if other factors are contributing. Other factors that might influence movements by toads include habitat quality, length of active season, prey availability or the need to find over-wintering sites that minimize the risk of freezing or desiccation. With the continued die-off of Western Toads in the Rocky Mountains, it is important to continue monitoring populations of Western Toads in other portions of their range to detect changes in their survival and recruitment. It is critical to assess basic natural history parameters as well as such acute issues as B.d. to provide a complete picture of Western Toad demographics. Information included in the present study will be helpful in determining the health and general life history patterns of other toad populations.

Acknowledgments.—A. Clark assisted with field work and identification of prey items. R Beckwith identified a portion of the prey items. J. Shepherd analyzed the data. D. Green (USGS National Wildlife Health Center) conducted necropsies on toads. U. Kelley provided information on suturing materials and techniques. J. Hayes, C. Pearl, M. Snook, and B. Wales reviewed a previous version of this manuscript. Funding was provided by the Pacific Northwest Research Station and U.S. Fish and Wildlife Service. Toads were handled under Oregon Permit Numbers 57-02, 47-03, 21-04, and 37-05.

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INTRODUCTION

Previous herpetological surveys performed in Armenia were generally focused on a wide range of questions encompassing the country’s fauna, including the morphology, systematics, natural history, and general ecology of reptiles (Chernov 1939; Darevsky 1957; Aghasyan 1996; Aslanyan 2004). However, there is a critical need for the acquisition of currently lacking detailed reptile distribution information for Goravan Sands Sanctuary. Previous assessments were presented without details of the methodology used (Aghasyan 1985; Danyelyan 1989). The need for accurate information to perform monitoring stimulated the need for this study.

The Goravan Sands Sanctuary is a sandy, semi-desert site in the Ararat region of Armenia (Fig 1). This site supports two reptile taxa of local and global conservation priority, the Persian Toad-headed Lizard (Phrynocephalus persicus, Fig. 2a) and the Mediterranean Tortoise (Testudo graeca, Fig. 2b) (Danielyan 1987; Baillie et al. 2004); as well as, a few common taxa such as Pleske’s and Shtraukh’s Racerunners (Eremias pleskei and Eremias strauchi, respectively, Fig. 2c, d), Striped Lizard (Lacerta strigata, Fig. 2e), and Montpellier Snake (Malpolon

HABITAT SUITABILITY FOR REPTILES IN THE GORAVAN SANDS SANCTUARY, ARMENIA

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Abstract.—The Goravan Sands Sanctuary is an important Armenian wildlife conservation area. The objectives of my study were to assess habitat suitability for reptiles within the sanctuary by comparing species richness, total abundance and species diversity across 35 random quadrats. I present the mean abundance data of 5 reptiles: Phrynocephalus persicus, Eremias pleskei, Eremias strauchi, Lacerta strigata and Testudo graeca. Maps of the relatively uncommon lizard P. persicus reflect species richness patterns whereas maps of the most abundant lizard E. pleskei more accurately reflect total reptile abundance and species diversity. About 71% of the area of the patches is covered with regions of high and moderate species diversity – suitable for reptile inhabitation. Fourteen percent of the area is covered with patches of low diversity. The moderate and highly suitable patches are recommended for intensive conservation management planning.

Key Words.—abundance; Armenia; habitat suitability; species diversity; interpolation maps; reptiles

FIGURE 1. Geographic location of The Goravan Sands Sanctuary in Armenia.

FIGURE 2. Representative photographs of reptiles from the Goravan Sands Sanctuary, Armenia: (a) Persian Toad-headed Lizard Phrynocephalus persicus; (b) Mediterranean Tortoise Testudo graeca; (c) Pleske's Racerunner Eremias pleskei; (d) Shtraukh's Racerunner Eremias strauchi; (e) Striped Lizard Lacerta strigata; and (f) Montpellier snake Malpolon monspessulanus. Photographed by Tigran L. Tadevosyan.
Tadevosyan-Inventory Goravan Sands Sanctuary, Armenia September 2006

The following objectives were targeted to justify future management planning: (1) determine the abundance, species richness, overall density and species diversity of reptiles in the study area; (2) produce interpolation maps to collate the reflection abilities; and (3) evaluate habitat suitability and delineate reptile distribution within the sanctuary.

### MATERIALS AND METHODS

#### Study area

According to remote sensing data, the Goravan Sands Sanctuary is composed of nearly 10 islets of sandy semi-desert habitat with a total area of nearly 175 ha. The dominant plants of the sandy habitats include semishrubs of *Noaea mucronata*, *Kochia prostrata* and *Achillea tenuifolia* (pers. obs.). The north sands are bordered by reclaimed land, and the other sides by dry limestone rocks covered with sparse shrubby vegetation called phryganoids (Takhtajyan and Fedorov 1972; Tadevosyan 2001). The boundaries of Goravan Sands Sanctuary are poorly defined. I conducted my study within the two largest plots of sands: main and eastern massifs (~136 ha, 894-965 m above sea level) that earlier investigators identified as part of the sanctuary (Tadevosyan 2001; Khanjyan 2004; A.V. Aslanyan’s, pers. comm.).

#### Sampling

We observed reptiles in 35 randomly selected 20 x 20 m quadrats using visual encounter surveys (Shenbrot and Krasnov 1997; Crump and Scott 2003; Heyek 2003a). Quadrat positions were determined using a digital map of the Goravan Sands Sanctuary produced using Arc View GIS v. 3.2.a (ESRI Inc., Redlands, California, USA). Relief and land cover data were obtained through vector analysis of a 1:25 000 topographic map (Anonymous 1979) and satellite image LandSat 7 ca. 2000 (NASA ES Ent., USA). The map and satellite image were geo-referenced in WGS-84, UTM (zone 38 N) coordinate system. I used Random Point Generator software (Jenniss 2005) to randomly generate 35 sampling plots. Point coordinates were uploaded into an Etrex GPS unit with accuracy averaging 5 m (Garmin Intern. Inc., Olathe, Kansas, USA) with DNR Garmin software (Minnesota Department of Natural Resources, Minnesota, USA).

We surveyed quadrats once in randomized order between 1000-1800 hrs in March-June 2005. I recorded the point coordinates of the search areas using the GPS unit. Capture was used to identify individuals. Specimens were captured and individually marked on

<table>
<thead>
<tr>
<th>Quadrats</th>
<th>Species Diversity and Density (Specimens/Quadrat)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N/N E (d.ddddd) N (d.ddddd) P. persicus E. strauchi E. pleskei L. strigata T. graeca (N2)</td>
</tr>
<tr>
<td>1</td>
<td>39.88825084 44.73345295 0 3 0 0 0 0 0.11</td>
</tr>
<tr>
<td>2</td>
<td>39.89191068 44.71953300 0 6 0 0 0 0 0.03</td>
</tr>
<tr>
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<td>39.89224085 44.73402286 0 2 0 0 0 0 0.25</td>
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<tr>
<td>4</td>
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</tr>
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<tr>
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<td>39.89117056 44.76953311 0 0 0 0 0 0 -</td>
</tr>
</tbody>
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<table>
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<th>specimens/Relative abundance (%)</th>
<th>16/&lt;14</th>
<th>26/&lt;23</th>
<th>70/&lt;61</th>
<th>1/&lt;1</th>
<th>1/&lt;1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>114 (100%) of individuals</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Table 1. Species diversity and densities of reptiles in 35 quadrats located in the Goravan Sands Sanctuary. Table includes numbers and coordinates of 35 sampling quadrats in decimal degrees, abundance per species, Calculated Hill’s index (N2), and relative abundance of species (%). E = East; N = North; N2 = Hill’s species diversity index.*
the ventrum with a felt tip marker and then released at the capture site.

**Statistical treatment.**—I calculated the mean abundance of each species per quadrat, total abundance of reptiles, simple species richness (species per quadrat), and Hill’s ($N_2$) index of species diversity (reciprocal of Simpson’s Index):

$$N_2 = \frac{1}{\sum p_i^2}$$

where $p_i$ is a proportion of individuals belonging to species collected (Hill, 1973; Schenbrot and Krasnov 1997). Mean ($M$), standard error ($SE$) and variation range ($R$) of abundance per species were calculated. Interspecific differences in abundance were analyzed using a single factor Kruskal-Wallis test, with the Fisher’s LSD post hoc testing. Associations among total abundance of reptiles, species richness, and ($N_2$) index of species diversity and the abundance of each species were analyzed using Spearman’s Rank correlation analysis ($R_{sp}$). Significance level for all tests was $P < 0.05$.

**Visual analysis.**—To perform visual analysis of spatial distribution diversity measures were interpolated once into values on the grid maps using Inverse Distance Weighted (IDW) interpolation (grid cell size = 20; neighbors = 12; power = 2), in Arc View GIS 3.2a and Arc View Spatial Analyst 2.0. I used the several classifications for grid mapping: three classes (one class for each additional species) for species richness; six classes (one class for every two additional specimens) for total reptile abundance, and six classes (one class for each 0.2 increase of the $N_2$ index) for species diversity. I manually converted grid patches from each class to vectors to measure and compare their areas. I used $N_2$ diversity index to finalize comparisons of the areas of patches because this index is a derivative of species richness and abundance. I used a standardized taxonomic nomenclature for the region (Ananjeva et al. 2004).

**RESULTS**

I mapped quadrat locations (Fig. 3) and specific locations are referenced by decimal degrees. The list of species, measured density values, and calculated $N_2$ per quadrat are given in Table 1. There were significant differences among species abundance detected ($n = 35; H = 37.04; df = 4; p < 0.001$). The data and particular differences between mean abundance of taxa are shown in Table 2. There was no significant correlation among species for abundance (Table 3). However, species richness was correlated with abundance of $P. persicus$ and $E. pleskey$ and with total reptile abundance and $N_2$ index. These variables were correlated with abundance of $E. pleskey$ and with each other. We found no $M. monspessulanus$ in studied quadrats. Interpolated grid maps of density per species are available at The Center for Ecological-Noosphere Studies, The National Academy of Sciences (CENS NAS RA) in Yerevan, Armenia.

![Figure 3](image-url)
Maps of species richness (Fig. 3a), total reptile abundance (Fig. 3b) and Hill’s (N_i) diversity index (Fig. 3c) show similarly spread patches with low, moderate and high levels of corresponding variables. According to the species richness value, quadrats were unified within 4 classes of patches while for total reptile abundance and diversity index (N_i), 6 classes of values were delineated. Hence, the map of species richness is less clear as it indicates two plots (1-2; Fig. 3a) of low richness and one plot with the highest richness (5a; Fig. 3a). In contrast, the map of total reptile abundance (Fig. 3b) shows the three plots with the lowest values were delineated. Hence, the map of species richness is three plots with low species diversity, excluding plot 5, which drew the same conclusions regarding habitat requirements of these species. Moreover, the low abundance of T. graeca, and absence of M. monspessulanus in samples may be due to my sampling methodology, because these species are sparsely distributed into dense aggregations. The snake M. monspessulanus occurs in microhabitats like open rocks, and with colonies of rodents (Meriones ssp.), which rarely coincide with random quadrats. Hence, the maps generally reflect habitat suitability for the three most common lizards.

The absence of significant correlations among the abundances of these taxa makes their use as indicator species for predicting the density of any other taxa of doubtful utility. In this respect, maps of generalized diversity measures like richness, total abundance and diversity may provide important information for conservation decision making. Using actual values of species abundance, richness, and diversity provided habitat suitability classifications that are more objective than most a priori classification schemes (Schenbrot and Krasnov 1997). More research is needed to clarify the roles of other microhabitat variables that were not used in this study.

Abundance of P. persicus was correlated with species richness, whereas abundance of E. pleskei was correlated with total abundance of lizards and N_i. This suggests that maps of species richness may best reflect the presence of relatively less abundant species, whereas the two other measures better illustrate the most

### TABLE 2. Significance of Differences Among Mean Abundance of Species. Significant p-values of Fisher’s LSD test are bolded.

<table>
<thead>
<tr>
<th>Taxon (mean abundance)</th>
<th>E. pleskei</th>
<th>E. strauchi</th>
<th>P. persicus</th>
<th>L. strigata</th>
<th>T. graeca</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. pleskei (n = 35; M ± SE = 2 ± 0.144; R = 0-8)</td>
<td>-</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>E. strauchi (n = 35; M ± SE = 0.743 ± 0.24; R = 0-6)</td>
<td>&lt;0.001</td>
<td>-</td>
<td>0.38</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>P. persicus (n = 35; M ± SE = 0.457 ± 0.14; R = 0-4)</td>
<td>&lt;0.001</td>
<td>0.38</td>
<td>-</td>
<td>0.19</td>
<td>0.19</td>
</tr>
<tr>
<td>L. strigata (n = 35; M ± SE = 0.0286 ± 0.029; R = 0-1)</td>
<td>&lt;0.001</td>
<td>&lt;0.03</td>
<td>0.19</td>
<td>-</td>
<td>1.00</td>
</tr>
<tr>
<td>T. graeca (n = 35; M ± SE = 0.0286 ± 0.029; R = 0-1)</td>
<td>&lt;0.001</td>
<td>&lt;0.03</td>
<td>0.19</td>
<td>1.00</td>
<td>-</td>
</tr>
</tbody>
</table>

This survey reveals that the three most abundant lizard species, E. pleskei, E. strauchi, and P. persicus, are distributed throughout the study area of the Goravan Sands Sanctuary; whereas, L. strigata and T. graeca are probably characteristic of neighboring reclaimed land and rocky habitat, respectively. Darevsky (1957), Tadevosyan (2001) and Aslanyan (2004) also

### TABLE 3. Spearman rank correlation matrix for measured variables: densities of P. persicus, E. strauchi, E. pleskei, L. strigata and calculated variables: Numbers of species, Total abundance of reptiles, and Hill’s species diversity index (N_i) at the Gorvan Sands Sanctuary, Armenia.

<table>
<thead>
<tr>
<th>Variables</th>
<th>P. persicus</th>
<th>E. strauchi</th>
<th>E. pleskei</th>
<th>L. strigata</th>
<th>T. graeca</th>
<th>Numbers of Species</th>
<th>Total abundance</th>
<th>Hill’s N_i index</th>
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</thead>
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<tr>
<td>P. persicus</td>
<td>1.00</td>
<td>-0.11;</td>
<td>-0.44;</td>
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<td>-0.11;</td>
<td>0.53;</td>
<td>0.13;</td>
<td>-0.002;</td>
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<td>p = 0.82</td>
<td>p = 0.51</td>
<td>p = 0.51</td>
<td>p = 0.01</td>
<td>p = 0.45</td>
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<td></td>
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<tr>
<td>E. strauchi</td>
<td>-0.11;</td>
<td>n = 35</td>
<td>n = 35</td>
<td>n = 35</td>
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<tr>
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<td>p = 0.52</td>
<td>p = 0.14</td>
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<tr>
<td>E. pleskei</td>
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<td>1.00</td>
<td>p = 0.35</td>
<td>p = 0.64</td>
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<td>n = 35</td>
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<td>p = 0.35</td>
<td>p = 0.87</td>
<td>p = 0.74</td>
<td>p = 0.3</td>
<td>p = 0.16</td>
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<tr>
<td>L. strigata</td>
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<td>p = 0.52</td>
<td>p = 0.35</td>
<td>p = 0.87</td>
<td>p = 0.74</td>
<td>p = 0.3</td>
<td>p = 0.16</td>
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<tr>
<td>T. graeca</td>
<td>n = 35</td>
<td>n = 35</td>
<td>n = 35</td>
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<td>p = 0.35</td>
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<td>Species Richness</td>
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<td>p = 0.14</td>
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<td>p = 0.74</td>
<td>p = 0.18</td>
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<tr>
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<tr>
<td>Total abundance</td>
<td>p = 0.45</td>
<td>p = 0.21</td>
<td>p &lt; 0.0001</td>
<td>p = 0.3</td>
<td>p = 0.92</td>
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<td>1.00</td>
<td>n = 31</td>
</tr>
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<tr>
<td>n = 35</td>
<td>p = 0.05</td>
<td>p = 0.0001</td>
<td>p = 0.16</td>
<td>p = 0.91</td>
<td>p &lt; 0.05</td>
<td>n = 31</td>
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abundant taxa. Conversely, maps of species diversity and total reptile abundance appear to better reflect details of spatial distribution of habitat suitability than does the map of species richness. Significant correlations among species richness, total abundance and diversity suggest that the three measures can be equally useful for mapping habitat. However, using all three variables may incorporate multicollinearity in to analyses and confound regression analysis. In general, patches of high and moderate diversity (\(X_2; 0.12-0.4\)) comprise about 71% of the sanctuary (Fig. 3c). These patches also represent locations with moderate to high species richness and total reptile abundance (Fig. 3a, b). Relatively low diversity (0.8-1) is characteristic of three patches covering about 14% of the area. Low total abundance is also characteristic of these patches, while species richness is lowest only in two of them. The largest patch of low diversity is located in the north-central part of the main sandy massif, in the zone down the clayey hill. Until the early 1990s, this area was forested with mulberry trees (Malus sp.) (local residents, pers. comm.). Two other patches are situated near the SW and NE boundaries of sandy habitats, close to active and neglected sand pits, respectively. Soil quality in these areas may partially explain the low abundance of lizards found in these zones. Further research will be required to evaluate the role of soil quality in determining lizard abundance at these sites. Previous studies demonstrate that reptile abundance may be suppressed by cattle grazing (Busack and Bury 1974; Berry 1978). Relatively low reptile abundance within eastern sandy massifs (Fig. 3b, #4) may be associated with extensive grazing within this site. There were no quadrats with diversity level of 0.4-0.8; hence, the corresponding patches on the map (Fig. 3c) should be considered as undetermined. Whereas maps of species richness and total reptile abundance (Fig. 3a, b) only reflect actual indices. Patches of merged and single quadrats with the lowest levels of richness (0-2), total abundance (0-2) and diversity (0.6-1) are presumably characteristic of poorly suitable habitat (1-3; Fig. 3a-c). Quadrats with moderate levels of richness (2-3), total abundance (2-4) and \(N_2\) (0.2-0.6) presumably form habitat patches with moderate suitability whereas quadrats with the highest levels of richness (3-4), total abundance (4-6) and diversity (0.012-0.2) presumably represent highly suitable habitat patches. (Fig. 3a-c, #1-3).

Sites with low diversity and other measured variables (i.e., low suitable sites) should be preliminarily excluded from planned conservation management actions (i.e., translocations of P. persicus and T. graeca). However, after determining low suitability of these sites, it may be useful to perform experimental habitat recovery actions (Moulton and Korbett, 1999; Kingsbury and Gibson 2002). Sites with moderate and high species diversity, richness and total abundance should be targeted for implementation of strong and flexible conservation management plans including, protection, monitoring, and public awareness. More extensive inventory activities may be needed at all sites to validate the results of this study.

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**LITERATURE CITED**


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