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Photograph by Stan Trauth

The Western Slimy Salamander (Plethodon albagula) *occurs in southern Missouri, Arkansas, Oklahoma and Texas. It is restricted to woodland habitats and is known to brood its clutch in caves and abandoned mines.*

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EDITORIALS AND ANNOUCEMENTS

NON-PEER REVIEW SECTION

DAWNING OF *HERPETOLOGICAL CONSERVATION AND BIOLOGY*: A SPECIAL WELCOME TO YOUR NEW JOURNAL

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Inception of a new journal in herpetology is a rare event. The first discussion of developing a journal with an emphasis on natural history and conservation occurred among a subset of us (McCallum, others), while at the 2005 joint annual meeting of the SSAR/HL/ASIH in Tampa, Florida. Some of the initial questions we posed for a new herpetological journal were as follows: (1) is there a need; (2) audience; and (3) support? If any one of these did not exist, then the concept should be abandoned or modified. We critically examined these questions through discussions with many individuals and informal surveys performed on the Partners in Amphibian and Reptile Conservation (PARC) listserver (parc@listserv.uga.edu) and other forums. Early on, it was obvious to us that there was strong demand for an outlet serving natural history, field ecology and conservation studies, especially descriptive investigations and management case studies that appeared to lack a home in other journals. The road traveled since those discussions has been fast paced, culminating in this 2006 launch of *Herpetological Conservation and Biology* (*HCB*).

By September 2005, we concluded that the herpetological community had several outlets for publishing these kinds of manuscripts, but competition was keen for publication space. While the kernel of a new journal started germinating, we were unconvinced that launching a new printed journal was either possible or necessary. The initial journal committee was composed of Stan Trauth, Bruce Bury and Malcolm McCallum, with Richard Wassersug joining the effort in late September. We discussed the possibility of using traditional publishers for the journal and approached three for information.

By October 2005, six more members joined the advisory board: David Sever, Brian Miller, Raymond Saumure, Joe Mitchell, Jeff Humphries, and Mike Plummer. The founding members (N = 10) provided much of the initial concept formulation for the group and the journal. Two members (B. Miller and M. McCallum) volunteered to act as the fist editorial staff. However, the method of publication remained a roadblock. We knew that financial difficulties hampered several other herpetology journals (e.g., *Herpetological Natural History* was ceasing publication), and overcoming the inherent fiscal problems of publishing required a different tactic.

At this time, R. Wassersug suggested we consider an electronic platform, and he provided an example of a recent publication from *Nature*. We investigated electronic publishing and discovered that there were many high profile electronic journals being developed, and both the new generation of herpetologists and most established scientists were highly receptive to an online publication. A survey to the PARC listserver revealed overwhelming support for an electronic herpetological journal and several suggested that a number of hard (printed) copies should be generated and housed at academic institutions or high-profile museums. Also, it was clear that electronic publishing would provide us with a method of preventing manuscript backlogs, while remaining low cost.

In November, one of us (B. Bury) recommended making the journal open access (i.e., available online and free to authors). In December, we ran a series of surveys to determine if open access or page charges were desirable for funding a journal. Several respondents suggested that an *e*-journal could be inexpensive because the publishing costs are minimal (e.g., costs for data storage are low). Thus, the Advisory Board decided to focus on an open use journal with no costs to authors. We agreed not to request page charges or access fees for the electronic version.

From the outset, we wished to complement the existing printed journals in herpetology and conservation biology, of which we are strong supporters. For example, several of our "senior" editors have been members of *Herpetologica* for 5 decades and the *Journal of Herpetology* since its inception in 1968. Two of our editorial board members authored papers in Journal of Herpetology in its first year (Bury 1968; Stewart 1968). Many of those serving on our editorial board are members, editors or elected officials (now or earlier) of all the major herpetological journals. Our goal is to expand publication of worthy material on natural history, field ecology, conservation and management of amphibians and reptiles. These papers will appear in electronic format and, we trust, will not influence publication in other journals. We

FIGURE 1. Photograph of attendees at the first organizational meeting of *Herpetological Conservation and Biology*, Henderson, NV, on 2-3 June 2006. Left to right: Standing - Stan Trauth, Bruce Bury, Malcolm McCallum, Roger Luckenbach, Phil Medica, and Raymond Saumure; Sitting - Gwen Bury and Dave Germano. Photographed by Stan Trauth.

decided to welcome in-depth scientific articles (no news notes) as well as broader implications of studies on conservation and management issues. We opened the door for critical reviews (**Forum**) and well-thought-out reviews (**HerpSpectives**). These carve a niche somewhat different from other current publications. There is some overlap, but a little competition never hurt anyone. Still, our goals and electronic publication differ from most other outlets.

Further, we also determined that we will publish each issue of the journal as a single print volume at the end of each year. These will be available at or near production cost but our intent is to limit distribution to select university and museum libraries. This allows permanent storage of hard copies.

In December, David Germano and Erin Muths joined as Associate Editors. The journal Advisory Board exploded to 29 members in January 2006. Our email boxes quickly filled as members began actively brainstorming on various operating and logistical issues. We also developed a mock website that was eventually refined into our current site.

In February, several major organizational events defined our new path. Whit Gibbons joined the advisory board, and the total number of members was expanded to 36. He kindly forwarded the journal concept to the PARC Executive Board to encourage their support. We were asked to submit a formal proposal to PARC to cement a close tie of the groups. In March, PARC agreed to a teaming of PARC and *HCB*, which has proven mutually beneficial for both organizations. About this time, Raymond Saumure drafted the ‘Instructions for Authors,’ for *HCB* and the members provided input leading to the current version. We also began receiving inquiries about publishing in *HCB*, but we were not ready to accept manuscripts.

By April, we had 46 editorial members including Executive, Associate, Assistant and Advisory Editors. The large editorial staff was designed on purpose to minimize workloads on any one editor. Our goal for editorial staff is that the Associate Editors should handle no more than 15 manuscripts per year. As submission rates rise in the future, so will the number of editors.

We also established a new position of Assistant Editor, who we call an editor-in-training. These individuals have little prior editorial experience and are often beginning their professional scientific careers. They are assigned to senior editors who serve as their mentors. Our goal here was to cultivate strong editors for the future that can fill future staff vacancies and ensure the sustained health and growth of *HCB.* In about a year, we intend to reassess this position along with the other ones to ensure each is effective and of value to the journal and its supporters.

On 14 April 2006, we released our first call for papers, including posting on the PARC listserv. In the first 10 days, the website received >1000 visits from over 39 countries. Although most visitors were from the United States, United Kingdom, and Canada, the number of inquiries from foreign countries was surprising. We quickly began receiving manuscripts, and the peer review process proceeded. We also invited submissions from Henry Fitch and Hobart Smith—two icons of herpetology—that we respect, and both accepted our offer. We point out that these two herpetologists were contributors to the first issue of the new journal *Herpetologica* (Smith 1936a, b; Fitch 1939a, b).

We held the first organizational meeting of *HCB* on 2-3 June 2006, at the USGS Field Office in Henderson, Nevada (organized by B. Bury and hosted by Phil Medica). The meeting was highly productive as the collective group (Fig. 1) made many unanimous decisions regarding journal workings and management (Table 1). Some topics were too complex to decide at the time and were tabled (e.g., having elected officials). Several attendees had known each other for decades while others had never met in person, although all the key members had corresponded many times via email. To encourage some comradeship (and interest in field ecology), we also took a late afternoon/evening field trip to the Kelso Dunes and vicinity in the eastern Mojave Desert, California. We enjoyed reminisces and knowledge by Roger Luckenbach, who conducted surveys in the area in the 1970s (e.g.,

TABLE 1. List of measures, issues and policy decisions at the meeting of *Herpetological Conservation and Biology*, Henderson, NV, on 2-3 June 2006. Votes were by both the SC = Steering Committee present (n = 5) and All = all attending (n = 9). Y = Yes, motion passed; T = Tabled; discuss at the next meeting.

Issue Voted On	SC	All
Policy and Direction		
Accept Rule of Order: each passed measure must receive a majority vote of members present at the meeting (those on Steering Committee, Executive Committee and Associate Editors; n = 5); and record vote of all *HCB* members present (n = 9).	Y	Y
Accept offer by S. Trauth to investigate establishing a non-profit foundation to handle all finances as well as non-profit status for the journal.	Y	Y
Accept offer by S. Trauth to serve as the archivist/historian, and deal with libraries and museums for the archive.	Y	Y
Add name "International" to the definition and scope of *HCB*	Y	Y
Continue discussion to establish a partnership with the World Congress of Herpetology	Y	Y
Change name of the "International Board of Advisors" to the "Editorial Guild".	Y	Y
Accept proposal to develop a new organizational structure with elected officials (e.g., President, Board of Directors, etc.).	T	T
Journal Development and Production		
Publish Journal a minimum of 2 times per calendar year with goal of 4/yr	Y	Y
Inform authors that once there is final acceptance, the paper will be published in the next available issue.	Y	Y
Release first issue when the Steering Committee is satisfied that the contents are sufficient to represent a solid issue.	Y	Y
Develop a "flash list" to announce release of each new issue (online version).	Y	Y

Luckenbach 1975, 1982). All members left the meeting and field foray confident that everyone was on the same page.

After several discussions with Aaron Bauer, President Elect of the World Congress of Herpetology, this group also agreed in late June to partner with *HCB*. Along with ties to PARC, this was another defining moment in our brief history. The involvement of the World Congress provides an opportunity for *HCB* to become the first truly international journal in herpetology. We are currently working with the World Congress to expand the editorial staff to include the entire international community. Although our editorial staff included members from around the world, most are from North America. We hope to change this landscape with a major expansion or reorganization of the editorial staff. To remain abreast with the latest happenings, please visit our webpage: www.herpconbio.org.

Although there are many intricacies in journal operations that continue to bedevil us, in a little more than one year *HCB* evolved from an idea to an operational journal. To us, it is incredible that so many individuals volunteered to develop a common effort. We think this demonstrates the need, audience, and support for a new herpetological journal that is on line.

We hope that all who use this journal for publication, information, learning or recreation, will appreciate the amount of work that was devoted by so many individuals. This is a group effort and it will only be as good as the time we devote to it. We also hope that this journal will become an important resource for all those who work diligently to investigate, conserve, and manage herpetofauna populations around the world. They need our help.

With the support and encouragement of the global herpetological community, there can be no doubt that this journal will flourish due to the readership and sacrifices of time by the Editorial Board. The development into one of the premier herpetological outlets at a later time lies with your continued interest and support. Now that we have launched this e-journal, we wish to hear your comments and suggestions to improve it or the group.

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ECOLOGICAL SUCCESSION ON A NATURAL AREA IN NORTHEASTERN KANSAS FROM 1948 TO 2006

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Abstract.—**Long-term ecological studies provide important information applicable to the conservation, management and restoration of native ecosystems. These studies allow us to observe changes in habitat and the correlated changes in associated amphibian and reptile communities. Research over the last 58 years at the Fitch Natural History Reservation has indicated biotic responses that would likely have been imperceptible over the short-term. New investigators are encouraged to conduct long-term studies and institutions must devise ways to foster these activities.**

Key Words.—long-term research, ecological succession, herpetology

The University of Kansas Natural History Reservation, where I have spent the last 58 years of my life, exemplifies the benefits of long-term studies and the misconceptions that can result from relatively short-term efforts. The Reservation is a 239-hectare area in northeastern Kansas on the eastern edge of the Deciduous Forest Biome and its Oak-Hickory Association (Shelford 1963). Before my arrival in 1948, the tract had been used for grazing of livestock and cultivation of crops, and there were many fenced (barbed wire and rock wall) subdivisions. About half of the area had been devoted to the pasturing of cattle and horses (and sheep at an earlier stage) and consisted of a grass-weed mixture with little arborescent vegetation. After the area was designated as a Natural History Reservation in 1947, anthropogenic disturbance was largely limited to the lab buildings, residence and surrounding lawn, driveway, and scattered trails that were cleared with a machete (Fig. 1A). Domesticated animals, including grazing livestock, were prohibited. Fire was excluded.

The most obvious change on the Reservation since 1948 has been the widespread intrusion of dense woody vegetation (Fig. 1B; Fitch et al. 2001) a well-documented result of suppression of fire and grazing (Heisler et al. 2003; Knapp et al. 1998). My field work was mostly confined to the Reservation in the early years of sampling. Faunal composition changed as originally open areas acquired trees, and snakes became progressively scarcer. As catches dwindled, my responses typically included a shift to new areas for sampling and/or a change in collecting techniques. Diminishing returns, beginning in the late 1980's, encouraged me to shift my efforts to adjacent experimental areas of the University of Kansas (Fitch 2005, 2006), where grazing, burning, and mowing were regularly implemented. The experimental areas generally were in a stage of succession similar to that of the Reservation several decades earlier.

Most parts of the Reservation have undergone progressive change over the past 58 years, each of the areas expressing divergent rates of ecological succession. Least modified are the hilltops and slopes that already had the climax forest species, Chinquapin Oak (*Quercus muehlenbergii*), Black Oak *(Q. velutina*), Bur Oak (*Q. macrocarpa*), and Shagbark Hickory (*Carya ovata*). Also changing slowly, but less stable than the climax forest, was the mixed forest with some or all of the climax species growing in close association with Black Walnut (*Juglans nigra*), Common Hackberry (*Celtis occidentalis*) and American Elm (*Ulmus americana*). Early seral forest, which consisted mainly of Honey Locust (*Gleditsia triacanthos*) and Osage Orange (*Maclura pomifera*), was subject to relatively rapid change.

In the first year, grazed pastures reverted to a luxuriant grass-weed mixture. The grasses were composed primarily of two exotics, Smooth Brome (*Bromus inermis*) and Kentucky Bluegrass (*Poa pratensis*). Native species of the local tall-grass association, the bluestems, Indian Grass, and switchgrass were scarce. The most abundant weedy species were those that were noxious or otherwise resistant to the grazing of livestock. These included milkweeds (*Asclepias* sp.), Snow-on-the-mountain (*Euphorbia marginata*), Nettle Leaf Noseburn (*Tragia betonicifolia*), thistles (*Cirsium* sp.), Blackberry (*Rubus allegheniensis)*, Carolina Horse Nettle (*Solanum carolinense)*, Buffalo-bur Nightshade (*Solanum rostratum)*, Prickly Lettuce (*Lactuca serriola*), Cocklebur (*Xanthium strumarium*), and Hoary Vervain (*Verbena stricta*). The grass-weed association changed rapidly from year to year. Weedy species tolerant or resistant to grazing disappeared first, due to competition with grasses. After several years, there remained mainly a stand of Smooth Brome, which in turn was crowded out by thick stands of young trees (mostly elms).

Formerly cultivated fields developed a mixed stand of Giant Ragweed (*Ambrosia trifida*) and Sunflower (*Helianthus annuus*). Over a period of several years, a mixed weed association dominated by Goldenrod (*Solidago* sp*.*) flourished in these areas. As in the former pastures, this weed association was gradually replaced by young trees (*Ulmus* etc.).

All vertebrate species were drastically affected by these successional changes. In the first season after removal of grazing livestock, a population explosion occurred in the Prairie Vole (*Microtus ochrogaster*), which attained a density of hundreds per hectare. Its bird, mammal, and reptile predators thrived and increased. Reptiles were especially monitored to clarify their relationship to the changes that occurred. Live-traps were constructed of 6 mm wire “hardware cloth” shaped into cylinders 15.2 cm in diameter with an entrance funnel at one or both ends. Later, 1.2 x 0.6 m shelters of metal (corrugated roofing “tins”) or wood were used. These shelters were advantageous over the wire traps in that mortality of reptiles was never a factor. Also, reptiles using them for hiding places were much more likely to have food in their stomachs than their trap-caught counterparts.

Collecting effort for animals varied somewhat from year to

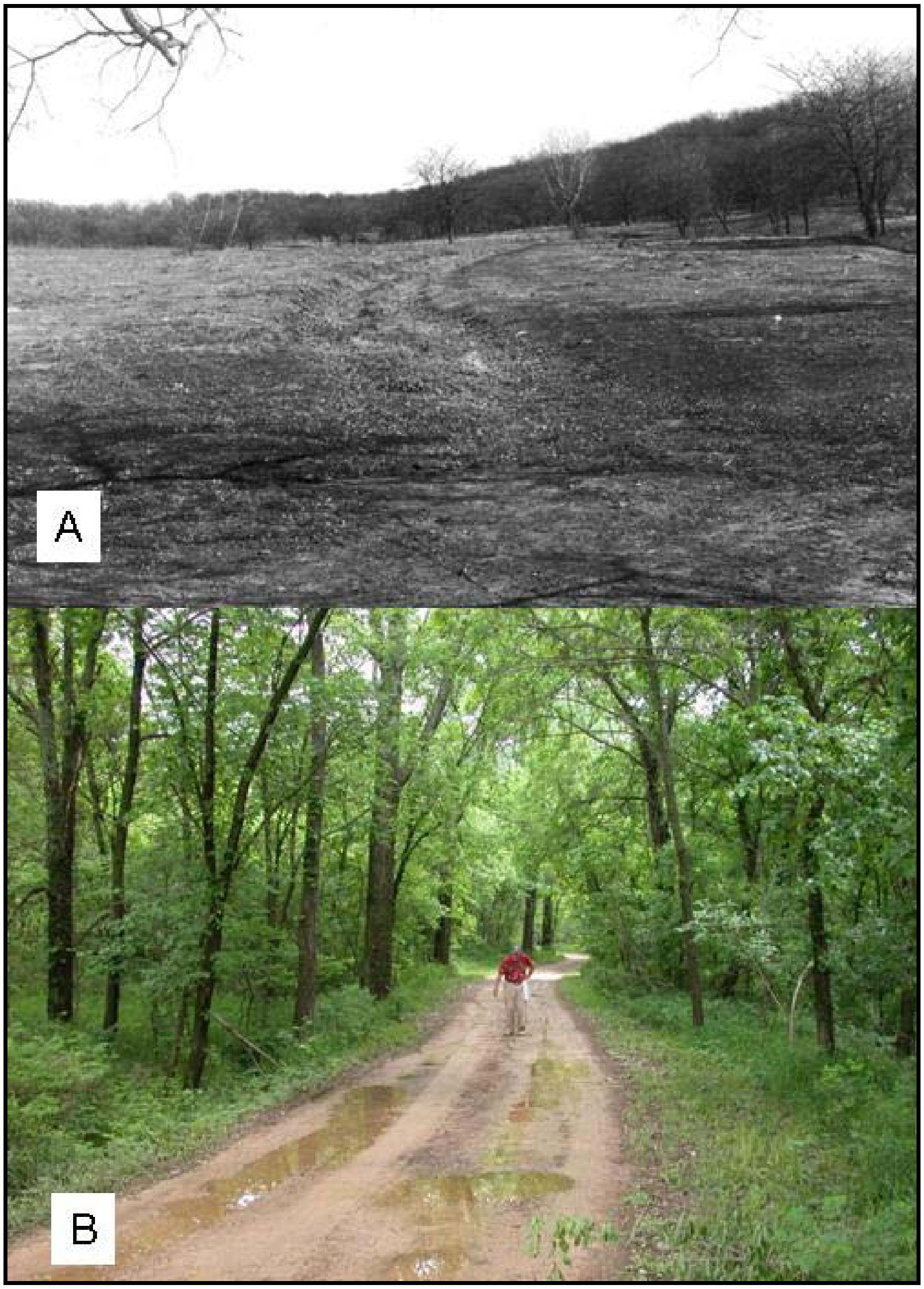

FIGURE 1. Entrance to Fitch Natural History Reservation in 1948 (A, photographed by W. Dean Kettle) and 2004 (B, photographed by Alice Echelle). The striking successional changes in vegetation were accompanied by equally remarkable modifications in the composition of the herpetofauna.

year and from decade to decade. During the first few years, the catch generally increased as more traps became available and as snake abundances increased under favorable conditions of food and cover. In the 1957 season, funnel traps with drift fences were added to the open areas comprising the snakes' summer habitat; whereas, in earlier years trapping had been limited to hilltop outcrops where the snakes came to hibernate in the fall months (Fitch 1965).

Every species of the local herpetofauna was drastically affected, with each species changing according to its own pattern (Fitch 2005). Table 1 shows species-specific catches of snakes (excluding recaptures) on the Reservation. It does not include those taken on the adjacent experimental areas. The table is included only to convey a rough approximation of general trends because the numbers are affected by unavoidable variables. Partial decades of collecting should not be considered as comparable to full decades. My efforts became more focused on the experimental areas as the herpetofauna declined on the Reservation, perhaps accentuating the impression of decreasing numbers on the Reservation. Also, numbers were affected by the previously mentioned shifts in trapping methods. In the 2001-2006 intervals, inevitable effects of aging curtailed my collecting intensity.

Responses of the various species to ecological succession can be broadly classified into several groups. Some of the species were early seral, and required bare soil, sand, rock or short grass.

TABLE 1. Numbers of snakes of each of 12 species processed per decade, from the 1940s into the 21st century on the Fitch Natural History Reservation. Recaptures are not included.

Species	1948-1949	1950s	1960s	1970s	1980s	1990s	2001-2006	Totals
Agkistrodon contortrix	44	773	436	455	534	37	6	2285
Carphophis vermis	7	169	161	33	9	23	0	402
Coluber constrictor	52	635	212	235	284	21	10	1449
Crotalus horridus	2	62	16	2	3	4	0	89
Diadophis punctatus	11	1430	1735	4090	4260	2195	193	13914
Lampropeltis calligaster	1	37	55	36	30	6	2	167
Lampropeltis triangulum	0	13	22	15	24	11	0	85
Nerodia sipedon	2	30	92	46	26	52	6	254
Pantherophis obsoletus	15	231	85	65	108	38	8	550
Pituophis catenifer	10	76	25	1	8	0	0	120
Storeria dekayi	0	23	164	32	23	15	0	257
Thamnophis sirtalis	25	313	788	359	447	448	98	2478
Totals	169	3792	3791	5369	5756	2850	323	22050

Among the first to disappear, members of this group were less useful in tracking succession than those that persisted longer. Most of the lizard species and also several amphibians were in this group, thus they are not represented in Table 1. This general category includes the Great Plains Skink (*Plestiodon obsoletus*), Five-lined Skink (*Plestiodon fasciatus*; still persists in 2006 around the residence and lab buildings), Six-lined Racerunner (*Aspidoscelis sexlineatus*), Ornate Box Turtle (*Terrapene ornata*), Woodhouse's Toad (*Bufo woodhousii*), Great Plains Narrowmouth Toad (*Gastrohryne olivacea*), Plains Spadefoot (*Spea bombifrons*), Prairie Skink (*Plestiodon septentrionalis*), and Flat-headed Snake (*Tantilla gracilis*). The last three species, never common and never occupying more than a small part of the area, were among the first to disappear. The other species of this group were initially at least moderately abundant, but most dwindled rapidly after cattle were removed.

The largest group comprised species that declined after livestock removal but then persisted for many years. Some of these are apparently no longer present on the area (Fitch 2006), including the Western Chorus Frog (*Pseudacris triseriata*), the Timber Rattlesnake (*Crotalus horridus*), and the Bullsnake (*Pituophis catenifer*). The two latter species were both fairly common in the beginning, but dwindled during the 1960s, and the few individuals found in later years were most likely vagrant. The last resident Timber Rattlesnakes were found in the 1960s at prominent limestone outcrops; the spread of deciduous trees in thick stands apparently eliminated critical basking places along the ledges.

Species that declined markedly but that still occur on the area include the Prairie Kingsnake (*Lampropeltis calligaster*), Little Brown Skink (*Scincella lateralis*), Slender Glass Lizard (*Ophisaurus attenuatus*), Prairie Ring-necked Snake (*Diadophis punctatus*), Eastern Yellow-bellied Racer (*Coluber constrictor*), and Osage Copperhead (*Agkistrodon contortrix*). The Prairie Kingsnake grew progressively scarcer, but is probably still present. *Scincella* occupied the grass-weed pastures on the Reservation rather than its usual leaf litter woodland habitat. It dwindled slowly but was still present in 2006. Although *Ophisaurus* was rare when the Reservation was created, it thrived after grazing livestock were removed, increasing from an initial nucleus of a few individuals to high abundance in the former pastures where tall grass had come to predominate. In the 17th year, it was so common that more than 70 were taken in a single day. By then, tree saplings had become established and were beginning to shade out the grasses. From the early 1960s, this species steadily lost ground, and by 2006, it was scarce although still present. *Diadophis punctatus*, at peak abundance, outnumbered all other reptile species combined. It has dwindled gradually but is still present in 2006 (Fitch and Echelle 2006). The Yellow-bellied Racer is a good example of a generalized snake. Unlike some of the other species, it is not dependent on one kind of prey; first-year young take orthopteran insects, and adults take mouse-sized rodents, common lizards or small snakes. However, *Coluber constrictor* dwindled gradually, and those found in recent years have been hatchlings, perhaps wanderers from other habitats. The copperhead increased for several years in response to increased cover and the abundance of the prairie vole, its favorite prey, but from the early 1950s, as voles began to decline, it underwent a downward trend that has lasted more than 50 years. Without the vole as food, snake litters are smaller and non-breeding is more common.

Several species are not easily classified in any of the above groups. One of these is the Red-sided Garter Snake (*Thamnophis sirtalis*). It increased rapidly and became abundant in the early years and is still thriving in 2006. The Northern Watersnake (*Nerodia sipedon*) was present at the pond throughout the years and seemed to be little affected by the changes in terrestrial habitats. The abrupt reduction in number of Black Ratsnakes (*Pantherophis obsoletus*) from the 1950s to the 1960s is due largely to the fact that, by the 1960s, a substantial proportion of those on the Reservation had been caught and marked; reduced captures in the 1990s can probably be explained by the shift of trapping effort to nearby experimental areas. The Brown Snake (*Storeria dekayi*) was most common during the 1960s and dwindled in later decades.

Superimposed on the changes precipitated by ecological succession, every species responded differently to environmental factors confronting it, and every year was unique in weather sequence. For example, environmental moisture was a critical factor for first-year young of the Red-sided Garter Snake. These depend almost entirely on earthworms for food. In drought years the availability of the worms is much reduced, depending on the severity of drought, and survival of young snakes is drastically affected. In a "bad year" only a small percentage may survive, and in these, sexual maturity may be postponed beyond the normal age.

As mentioned in Fitch (2006), it is ironic that on this area dedicated to preserving native flora and fauna and protected from anthropogenic disturbance for more than half a century, a large portion of the herpetofauna has been reduced by natural succession. However, perhaps it should not be surprising. The Reservation occupies the ecotone between eastern deciduous forest and tall-grass prairie. In this area, prairie is maintained as a fire or fire and grazing subclimax, and the balance can easily swing toward brush and forest when fire is suppressed. When the Reservation was created in 1947, it possessed a spectrum of habitat subdivisions and each was near, or adjoined, others of contrasting communities. Reptile/amphibian species thus had a choice of many habitats, all of them changing at different rates. Now, after 58 years of succession, the area as a whole is much different from what it was at the outset. The prospect is that over a sufficiently long time the fauna will become less diverse, different subdivisions will become more similar, and a climax community will eventually prevail. Some species, e.g., *Coluber constrictor*, which had shown marked decline on the Reservation, remained abundant on the experimental areas (Fitch et al. 2003). These areas thus provided perspective to the successional changes on the Reservation and demonstrated responses of the local ecosystem to management regimes such as mowing, fire, and grazing. To date, there are few published studies that have directly addressed the effects of brush management on native herpetofauna in the central United States (but see Jones et al. 2000). Effects of brush management have been more thoroughly studied for avian communities (e.g., Reinking 2005), and in some of these studies, reptilian responses are mentioned more or less incidentally (Shocat et al. 2005; Misenhelter and Rotenberry 2000).

In summary, observations of long-term changes in habitat and herpetofauna provide important information applicable to the conservation, management and restoration of native ecosystems. Without such observations, it would be difficult to surmise how these communities have changed or might change in the future. I have been fortunate to have the opportunity to conduct such studies. However, in the current atmosphere that fosters fast-return research supported by large grant money, long-term, detailed studies of natural history are generally not encouraged by academic institutions. This type of information is no longer solely pedagogical. Now, more than ever, we need a solid database to deal with the effects of human population growth and attendant problems of environmental alteration. Institutions need to promote detailed natural history research if only because the data can ultimately contribute to the management and conservation of biodiversity.

Acknowledgments.—I am indebted to many colleagues and students and also to family members for data included here. Although it is not practical to list all of the colleagues and students, major contributors included Donald R. Clark, Robert R. Fleet, Robert W. Henderson, Richard B. Loomis, Richard A. Seigel, and Donald H. Troyer. I am particularly grateful to my wife, Virginia R. Fitch, for support and help in many aspects of my work over the years. Alice F. Echelle typed the manuscript, and she and Anthony A. Echelle, and four anonymous reviewers read the manuscript and made helpful suggestions. Finally, I thank Stanley E. Trauth for honoring me with the invitation to contribute an essay to this promising new journal.

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Henry Sheldon Fitch was born 25 December 1909 in Utica, New York. Within a year after his birth, his family moved to the Rogue River Valley of southwestern Oregon where his parents had purchased a pear/apple orchard in the foothills of the Siskiyou Mountains. He received his B.A. from University of Oregon in 1930, and both the M.A. and Ph.D. degrees from University of California, Berkeley, in 1933 and 1937, respectively. He worked as a biologist for the U.S. Bureau of Biological Survey (U.S. Fish and Wildlife Service) at the San Joaquin Experimental Range in central California from 1938-1941 until he was drafted by the U.S. Army. After his release from the Army in 1945, he returned to his former job at the San Joaquin Range, but was transferred from California to Leesville, Louisiana in 1947. In 1948, the University of Kansas offered him a professorship position. His duties also included being resident naturalist and steward of the newly created University of Kansas Natural History Reservation, a 239-acre tract of land about seven miles northeast of Lawrence, Kansas. He still resides in this place that has been his home and living laboratory for the last 58 years. (Photographed by Vada Snider).

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DILEMMA OF NAME-RECOGNITION: WHY AND WHEN TO USE NEW COMBINATIONS OF SCIENTIFIC NAMES

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***Abstract.*—Recent changes in many scientific names have caused confusion for many non-systematists. We suggest wider use of the category of subgenus as a compromise between the simultaneous needs that exist at the present time: nomenclatural stability for the vast variety of users of scientific names, and phylogenetic correctness for systematists and others concerned.**

Key Words.—taxonomic changes; nomenclatural stability; subgenera; name usage

Recently, several long-accepted scientific names of numerous genera with world-wide or hemispheric distribution were split into two or more genera. Although most of these better represent the intricate relationships among groups of species within a genus in the broad sense (*sensu lato*), many biologists (especially those lacking taxonomic training) become confused by new taxonomic changes and are now uncertain how or what nomenclature is acceptable. An insurgence of new names has appeared with the increasing role of molecular genetic techniques and their inherent role in expressing phylogenetic relationships through genus-group names.

Examples of recent changes in nomenclature include revisions of *Eumeces* (Griffith et al. 2000; Schmitz et al. 2004), *Cnemidophorus* (Reeder et al. 2002), *Elaphe* (Utiger et al. 2002), and several changes in amphibian genera including *Bufo*, *Eleutherodactylus* and *Rana* (Frost et al. 2006). Each of these examples demonstrates one or more occasions where a long-known generic name perforce was restricted to the populations of a relatively small area including the range of the type species. The generic names of remaining new taxonomic subdivisions were either given new original names or provided resurrected ones from previous synonyms.

Frost et al. (2006) is an excellent example and includes a number of nomenclatural changes among North American anurans (Table 1). They split *Bufo* (*sensu lato*) into three genera, substitute *Craugastor* for *Eleutherodactylus* and *Lithobates* for some *Rana*, and revive *Syrrhophus.* Among these genera, *Bufo* and *Rana* have been previously accepted, well-known, and regularly used for over two centuries. During that time, zoologists produced an enormous literature-base referenced via these previously stable designations.

TABLE 1. Examples of prior and new names for North American anurans as proposed by Frost et al. (2006).

Earlier Name	New Combination
Eleutherodactylidae	
Eleutherodactylus augusti	*Craugastor augusti*
Eleutherodactylus guttilatus	*Syrrhopus guttilatus*
Bufonidae - true toads	
Bufo americanus	*Anaxyrus americanus*
Bufo boreas	*Anaxyrus boreas*
Bufo marinus	*Chaunus marinus*
Bufo alvarius	*Cranopsis alvaria*
Ranidae - true frog	
Rana catesbeiana	*Lithobates catesbeianus*
Rana chiricahuensis	*Lithobates chiricahuensis*
Rana aurora	*Rana aurora* [no change]
Rana boylii	*Rana boylii* [no change]

Concomitantly, nomenclatural changes have sometimes been widely disturbing to biologists, and perhaps this consternation is not necessary. More importantly, many fields of biology (e.g., physiology, medicine) have been accustomed to use of those names. Now must they, as well as field biologists, change all these names, especially when the change may have minor or nil importance to their fields? Here we offer an alternative.

Taxonomic nomenclature serves the primary function of name recognition and a secondary function of phylogenetic relationship. Taxonomic specialists are most concerned with the secondary function whereas other biologists are more concerned with the primary function of these designations. Splitting generic names in these cases serves only the *secondary* function of zoological nomenclature: to reveal relationships of species at a finer level than which biologists have been long accustomed. It does not serve the *primary* function of zoological nomenclature: name recognition.

Those two functions (relationship, name recognition) are inherent in the official "binominal" classification system (actually binary) in the fourth edition of the International Code of Zoological Nomenclature (Ride et al. 1999), hereinafter "the Code". The specific epithet (e.g., *pipiens* in the species name *Rana pipiens*) is attached permanently to its taxonomic category and remains valid barring problems for priority, as well as uncertainty of application to a given species. One name cannot be universally sufficient for name-recognition. A minimum of one other word is necessary to group species by binominal nomenclature into manageable units. The generic name serves that fundamental function, but it lends additional meaning in assembling species according to their phylogeny.

The degree to which phylogeny is reflected in generic names is subjective. The Code says nothing about evolutionary origin because that is a zoological, not nomenclatural, decision. Any of several generic names could be used in conjunction with a given specific epithet, without changing the latter's role as the ultimate recognition name; only the grouping name has changed. Obviously the name that functions to group related species should be kept as stable as possible, so that name recognition is minimally disrupted. As arbiters of nomenclature, taxonomists bear the responsibility of serving the needs for efficient name constancy of their fellow biologists and the needs of phylogeneticists to show evolutionary relationships of species to a reasonable degree.

We recommend a compromise to serve the needs of both of these important groups. The Code does provide for such a compromise, whereby the impact on stability of species names that result from the partitioning of any given genus can be greatly minimized by the optional subgenus category. As stated in the Code, names of subgenera, when used, follow in parentheses the generic name, providing the combination such as: the Marine Toad, *Bufo (Chaunus) marinus*. This option provides flexibility of the genus-group category without upsetting constancy of the species name.

The proposal of names at the subgeneric level is optional for the partitions of genera *sensu lato*, and the subsequent use of them. Thus one may use the name *Bufo marinus* without challenging the validity of the subgenus *Chaunus*. Although the partitions of *Bufo* and *Rana* in Frost et al. (2006) were proposed at the generic level, that does not prevent future workers from regarding them as subgenera. Thus the options exist, under the Code, to cite the names newly revived or created for the subdivisions of these two genera as genera or subgenera, and if the latter to use them only in circumstances where phylogeny is of concern, not necessarily in others.

This is a long-needed compromise between nomenclature's primary (name recognition) and secondary (phylogeny) roles. A century or more has passed without need for this compromise because most biologists were taxonomists. Today only a fraction of biologists are trained in systematics and even fewer conduct research in this area. When most users of names are taxonomists, name-recognition is not a major concern. When the primary users are non-taxonomists, as in modern times, name stability increases in importance.

Unofficially, custom plays an important role in what is acceptable or not acceptable. Customs stabilize, but also stultify. Subgenera have not been popular in the past, but changing times suggest that they could be an important component providing both phylogenetic correctness and name stability in modern systematics.

Those workers who prefer to retain current generic names in their broad sense are completely within their rights to do so, under the Code, and certainly no confusion is caused thereby. However, approval by others of these individual rights is ultimately vital. The compromise here suggested is fully justified, in our opinion, but it is operative only if accepted by those most concerned with phylogeny and the most recent scientific discoveries, as well as by those most concerned with stability. Individual rights need general acceptance.

A broad-based survey of preference by all users of the names under consideration would undoubtedly strongly favor stability. Taxonomic specialists have been slow to accept their responsibility to such users equally as well as to their responsibility to convey new knowledge of phylogeny. Acceptance of subgenera as a concession to all users is their part in the suggested compromise.

We appeal to the compilers of checklists that serve as name standards to recognize the need for the suggested compromise and incorporate subgeneric names in their listings, thereby validating the option of use of them, or not, by writers of every variety.

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Hobart Muir Smith (long sleeve plaid shirt) was born Frederick William Stouffer in Stanwood, IA on 26 September 1912, the sixth child of Harry and Blanche Stouffer, farmers who soon moved to Ohio. After Harry was killed in WWI, the children were orphaned and young Frederick was adopted by Charles and Frances Muir Smith, postal worker and teacher, respectively, who changed the boy's name to Hobart and took him to Oklahoma (Shawnee and Okmulgie) and later to Bentonville, Arkansas, where Hobart went to high school. He was sent to Kansas State University in 1928, where he majored in entomology, graduating with that major in 1932. During this time, Hobart met an older student, Howard Gloyd, and accompanied him on several summer field trips, discovering a new fascination with herps as well as a new intellectual orientation which included Gloyd telling HMS to look up a young professor, Edward Taylor, at the University of Kansas. The rest of Hobart's career from his Ph.D. in 1935 is generally well known, as is his hyperscrivenous reputation, with 1602 titles on his vita and some ten more in press, including two books with Julio Lemos-Espiñal. Asked to identify his most important publications, he quickly pointed to the Handbook of Lizards (1946) and the three checklists to Mexican herps (1943, 1948, 1950). With a smile and a raised eyebrow he also mentioned that the Golden Nature Guide has sold over a million copies. (Contributed by David Chiszar).

David Alfred Chiszar (short sleeve shirt) was born at a military base in Sergeant's Bluff, IA, 21 October 1944, to Alfred and Florence Chiszar, but the birth was officially recorded in Sioux City. He was moved to the family home in Perth Amboy, NJ, when Alfred was shipped to Europe as an Army Air Corps aviator. After WWII, Alfred worked for General Motors Corp. and later operated a Gulf filling station and mechanic shop, while Florence operated a confectionary store. The family continued these businesses for many years, but moved to Woodbridge, NJ, where David went to high school. Degrees in psychology came from Rutgers (BA 1966, Ph.D. 1970) and it was in 1970 that he met Hobart at the University of Colorado. Collaborative field and laboratory work followed, continuing to the present. Experiments on strike-induced chemosensory searching in rattlesnakes occupied much of their time, but they managed to make numerous field-collections trips within Colorado, surrounding states, and Mexico.

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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; Goosem 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 (Rodda 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

(*Gopherus agassizii*), Northern Diamondback Terrapin (*Malaclemys terrapin terrapin*) (Szerlag and McRobert 2006), Gopher Tortoise (*Gopherus polyphemus*) (McRae et al. 1981; Boarman and Sazaki 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*) (Wygoda 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, curbs, 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 depredation 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)

TABLE 1. Potential biases associated with using roads surveys to draw inference about turtle populations.

Biases	Effect
Abundance estimates	
Influenced only by individuals found on the road	Sample may not be representative of the local population
Individuals may be attracted to the road	Abundance estimates will be inflated
Road mortality and predators may limit populations	Abundance estimates will be low
Features associated with the road may prohibit animals from crossing	Abundance estimates will be low
Essential to mark individuals observed	Processing time and effort will be increased
Community descriptions	
Small species will not be observed as readily	Certain species will not be represented in their true proportion
Cryptic species will not be observed as readily	Certain species will not be represented in their true proportion
Habitat specialists may not be observed along roads	Certain species will not be represented in their true proportion
Demographic parameters	
Small individuals will not be observed as readily	Age class distribution will be biased towards adults
Disparate movements between the sexes	A population's sex ratio will be biased towards a particular sex that moves more
General	
Seasonality of movements	Observations may not be representative of the population on a year-round basis
	Between year comparisons may not be valid if weather conditions or sampling season differed

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.

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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 2002b). 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 (Davis 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 crowns 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

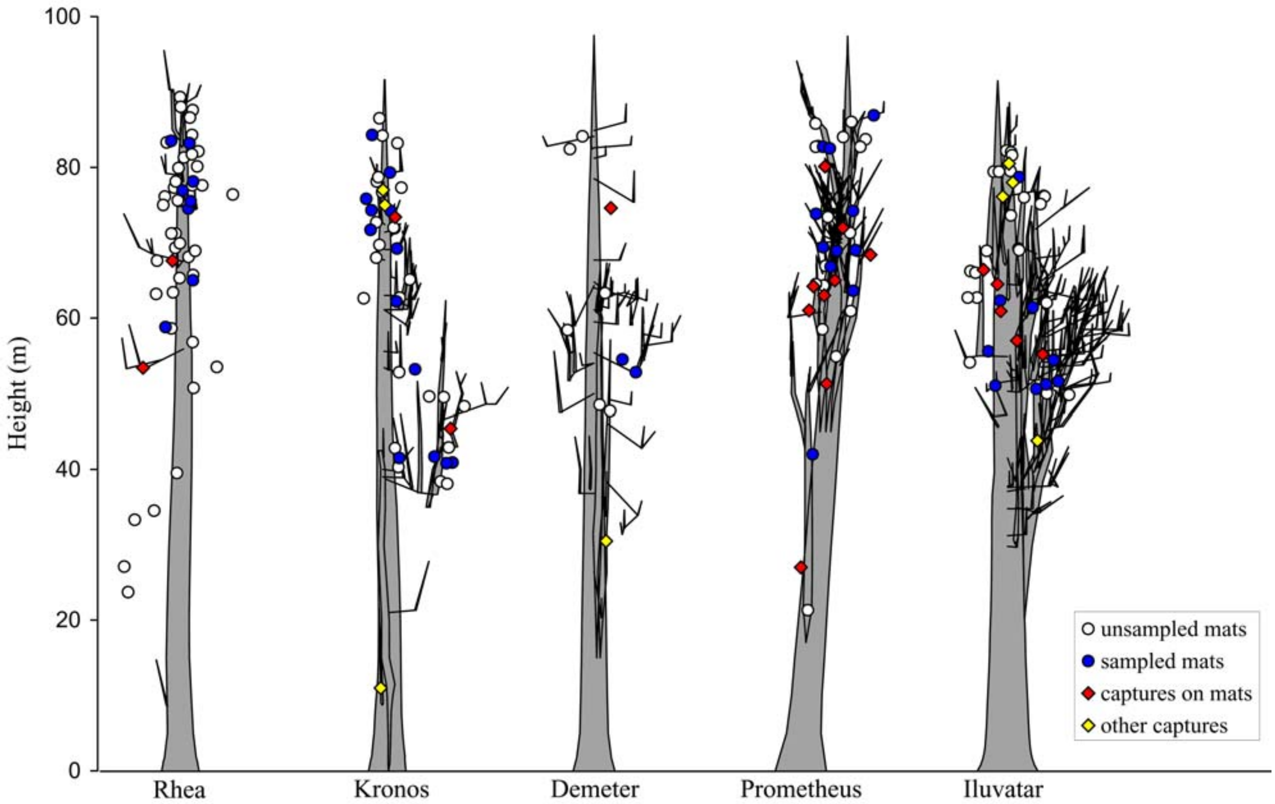

FIGURE 1. A two-dimensional display (view angle = 120°) of the three-dimensional crown structure of five redwood trees surveyed in this study. Main trunks and reiterated trunks are shaded gray. Limbs are indicated by thin, black lines. No branches are shown. Locations of *Polypodium scouleri* fern mats and *Aneides vagrans* captures are shown according to the legend. Note that "floating" symbols indicate locations on branches. "Sampled mats" are fern mats that were selected for placement of cover objects.

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.

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

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 reiterations arising from the main trunk or other 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 reiterations arising from limbs 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:

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

In each tree, we also determined the XYZ coordinates of all *P. 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:

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

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):

$$\text{Total mass (kg)} = 32.912 \times \text{mat volume} + 0.0250 \times \text{maximum frond length}.$$

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 nestling 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 x 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 alpha-numeric 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.

TABLE 2. Estimated sizes of *Aneides vagrans* populations on large redwood trees over two years derived from mark-recapture data using the Chapman (1951) method (see Chao and Huggins 2005). Numbers in parentheses are one standard error. Estimates are only for the portion of the arboreal population using fern mats.

	Salamander Abundance	
Tree	**January 2002**	**January 2003**
Prometheus	11 (0)	29 (8)
Iluvatar	11 (2)	20 (11)
Kronos	8 (4)	–
Five trees combined	54 (15)	–

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 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 marked or 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 mat 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 ($R^2 = 0.85$, $P < 0.0001$), area covered by litter bags ($R^2 = 0.38$, $P < 0.0001$), fern mat mass ($R^2 = 0.28$, $P <0.0001$), and fern mat area ($R^2 = 0.22$, $P < 0.0001$). 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 had apparently taken 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 that 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 douglasii*) 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 little or no wind. The two salamanders were observed throughout the spring and summer with the last observation occurring on 21 September 2002, when "evenings became too cold for foraging."

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 County, 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; McCranie 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;

Sillett and Van Pelt, unpubl. data). Compared to those on branches or limbs, fern mats in crotches hold more water per unit mass and store water longer (Sillett and Van Pelt, unpubl. data). Furthermore, soils in crotches have higher bulk densities and lower hydraulic conductances than soils on branches or limbs (Enloe et al. 2006), providing relatively stable refugia from desiccation during the dry season. Trees with soil in deep crotches likely provide suitably moist arboreal habitats for the year-round occupancy of old-growth redwood forest canopies by *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 collembolans 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 (Parker 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 over-winter 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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A Wandering Salamander (Aneides vagrans) from Humboldt County, California (United States). (Photograph by: William Leonard, ©2004. All Rights Reserved.)

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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 numbers, populations 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. hemiophrys 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 (*Pinus contorta*) in Glacier National Park and not in adjacent unburned areas (Pilliod 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 (*Oncorhynchus mykiss*) or Brook Trout (*Salvelinus frontinalis*). 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 satin 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 missing, and we searched within a 4-km radius of the last known location driving all roads to detect a signal. In 2002, missing toads were located with a fixed wing airplane, but funding restrictions limited this to the first year. All missing toads were located when aerial searches were used, even though ground searches failed to locate them. Missing toads could have moved outside the range of detection, been carried away by a predator, the transmitter could have quit due to a mechanical failure or due to damage from a predator.

Assays for B.d. employed swab samples of the first 10 male and 10 female toads captured (if available) at the breeding site in each study area in 2005 using techniques described by Livo (2004). Samples were sent to Pisces Molecular (Boulder, Colorado, USA) where a polymerase chain reaction (PCR) assay (Annis et al. 2004) was used to determine the presence of B.d. In 2004, five dead radio-tagged toads with no evidence of predation or injury were sent to the National Wildlife Health Center in Madison, Wisconsin for necropsies, as well as bacterial and fungal cultures (U.S. Geological Survey 2004).

Movements.—To investigate movement distances and potential routes, I recorded global positioning system (GPS) coordinates for each toad location. For each toad that was monitored for at least 7 weeks, I calculated the maximum distance traveled and straight line direction from the breeding site where all toads were captured. Seven weeks was selected as the minimum time period because toads reached their summer habitat within 7 weeks in 2002 and 2003. I determined that summer habitat had been reached when movements within a week did not exceed 150 m. The rate of movement (reported in m/day) was determined by dividing the distance traveled by the number of days between when the toad left the breeding site and arrived at the summer habitat. This measurement was an approximation because toads were located once or twice a week during breeding, and the exact day that toads left the breeding site was not known. The maximum distances traveled and rate of movement were compared between males and females using *t*-tests. The maximum distances traveled by toads in burned and green forests were also compared using *t*-tests at Fish and Twin where extensive burns occurred.

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, stem initiation, stem exclusion, young multi-stage, or old multi-stage (Oliver and Larson 1990). Harvest activity (Balm only) 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 when 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 re-sampling 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 1. Recapture rate and mean (range) measurements of SVL (snout-vent length), mass, and maximum movements within 6 months of male and female Western Toads PIT-tagged in five study areas in northeastern Oregon, 2002-2005.

	STUDY AREA				
Characteristic	**Balm**	**Twin**	**Fish**	**Crawfish**	**Lilypad**
Females					
SVL	104 (73-126)	119(115-123)	102(86-130)	101(95-107)	93(91-96)
Mass	117(44-234)	130(120-141)	105(56-185)	102(94-110)	71(60-79)
n	383	2	80	3	4
Males					
SVL	95(63-125)	93(79-103)	90(69-110)	87(80-94)	83(38-94)
Mass	72(28-145)	64(40-84)	64(32-112)	57(46-74)	53(38-85)
n	722	14	513	18	30
Female:male ratio	0.53	0.14	0.16	0.16	0.13
Recapture rate					
Females	2%[a]	-	3%[b]	-	-
Males	3%	-	34%	12%	37%
Distance (m) traveled					
Females	2823(180-6230)	2270(2110-2430)	2067(260-3560)	1670	-
n	17	2	7	1	0
Males	1390(350-3870)	530 (220-1130)	1248(390-2180)	537(340-730)	700(360-930)
n	9	4	6	3	6
Years monitored	2003-05	2002	2002, 2004-05	2003-05	2003-05

[a] Represents two females that were gravid in two consecutive years, and two females that were gravid in 2003 and in 2005.

[b] 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 (U.S. Geological Survey 2004).

***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

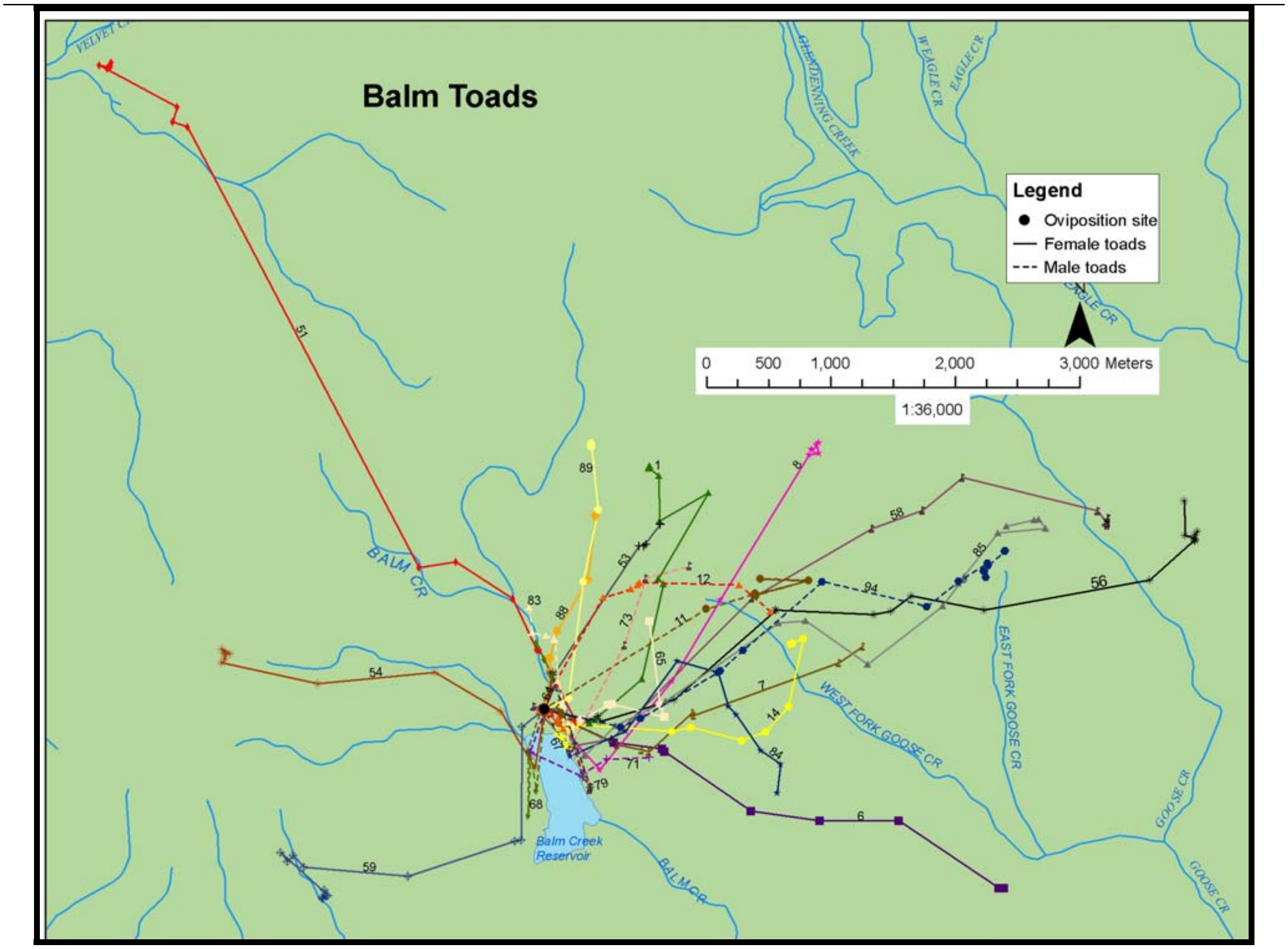

FIGURE 1. Locations of toads monitored more than 7 weeks at Balm study area in northeastern Oregon from 2003-2004. Numbered lines correlate to individual toads and their travel routes.

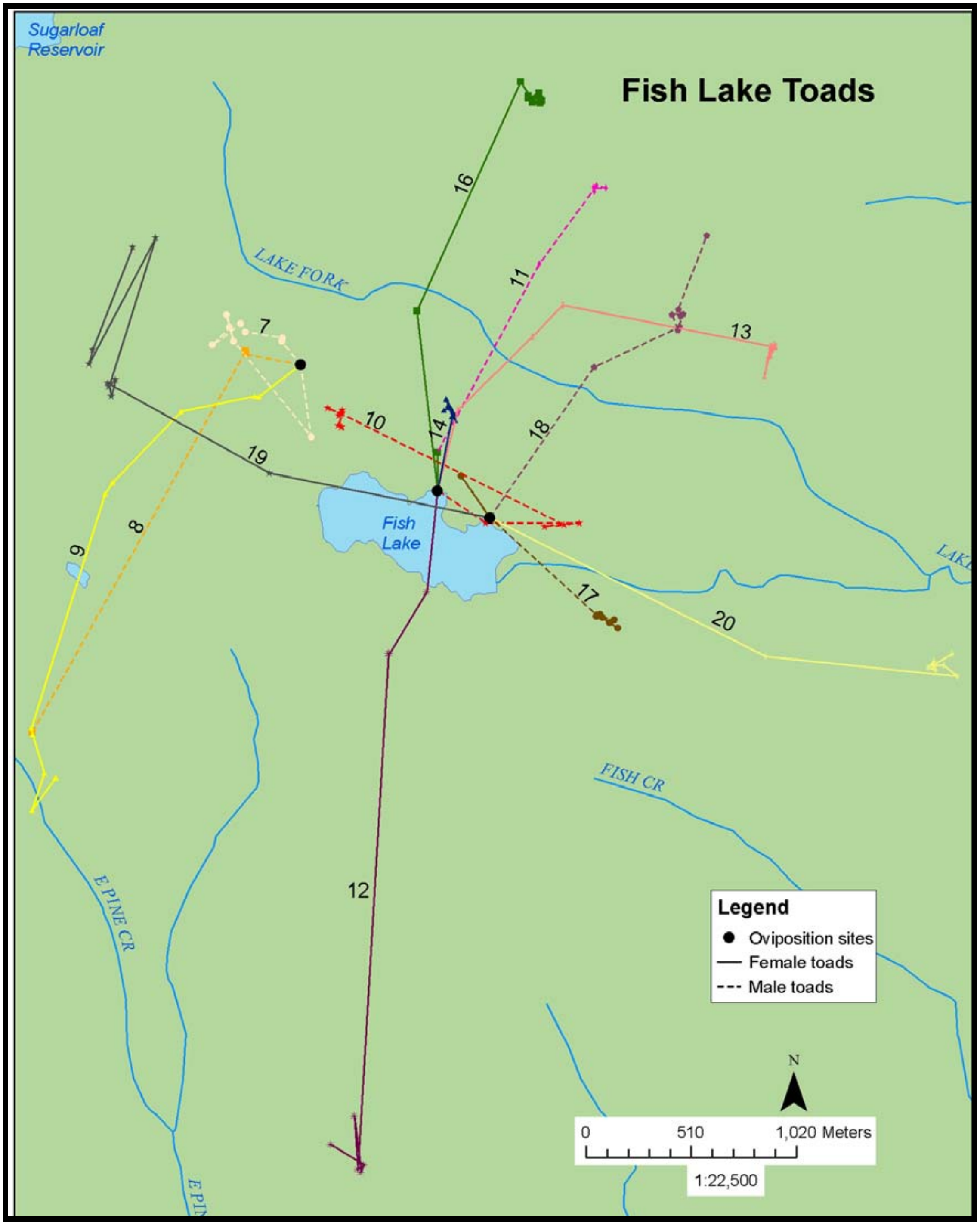

FIGURE 2. Locations of toads monitored more than 7 weeks at Fish study area in northeastern Oregon from 2003-2004. Numbered lines correlate to individual toads and their travel routes.

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).

	STUDY AREA					
	Balm	Twin	Fish	Crawfish	Lilypad	Total (%)
Alive	16%	83%	79%	20%	38%	32
Total predation	37%	0	21%	0	23%	29
Avian/mammalian	33%	0	21%	0	23%	27
Snake	3%	0	0	0	0	2
Radio off or redation[a]	16%	0	0	40%	8%	13
Dead, not predation[b]	11%	17%	0	0	0	8
Missing[c]	16%	0	0	40%	31%	16
Other[d]	3%	0	0	0	0	2
No. radio-tagged toads	62	6	14	5	13	100
Year of monitoring	**2003-04**	**2002**	**2002**	**2003**	**2003**	

[a] Toads may have slipped their transmitters or been consumed by a predator.

[b] Three of these toads were confirmed as having died of *B. dendrobatidis* and another five were too desiccated to determine fungal infection.

[c] 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.

[d] One toad was run over on a gravel road, and one toad died after it became entangled in vegetation.

hillsides with 60 percent slopes. Many toads followed small drainages with temporary runoff water or streams for a portion of their movements (Fig. 1, 2).

No male (N = 13) or female (N = 13) toads returned to their respective breeding sites during the summer, although four males at Fish and Twin moved 20-550 m to within 50 m of the breeding site by October 2002. Distance of males from the breeding site in November varied by study area; males at Lilypad and Crawfish were 240-920 m (n = 5) from the breeding site and males at Balm were 2028 and 3870 m (n = 2) from the breeding site.

A comparison of movements of toads in the two study areas with extensive amounts of burned forests (Fish and Twin) showed that females (n = 6) in burned forests traveled shorter distances (mean = 1807 m, SE = 328.5) than females (n=3) in green forests (mean = 2723 m, SE = 433.2). At the same two study areas, males (n = 8) in burns traveled a mean of 826 m (SE = 206.7) and males (n = 2) in green forests traveled 1500 m (SE = 961.7); these values were not significantly different (females: t = -1.64, df = 558, P = 0.14; males: t = -1.32, df = 509, P = 0.22).

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 m 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.

Variable	Toad	Random	F value	*P* value
Canopy closure (%)	25 (1.25)	42 (1.50)	65.34	< 0.01
Distance to water (m)	46 (3.70)	133 (5.79)	154.24	< 0.01
Distance to burrow (cm)	29 (4.57)	372 (28.07)	146.32	< 0.01
Distance to green forest (m)	68 (6.74)	92 (10.6)	3.88	0.05
Stems < 20 cm dbh	5.4 (0.42)	8.4 (0.54)	22.47	< 0.01
Stems ≥ 20 cm dbh	0.5 (0.04)	1.5 (0.8)	128.66	< 0.01
Ground cover (%)				
Bare ground	23 (0.92)	32 (2.86)	7.83	< 0.01
Grass	117 (0.73)	16 (0.78)	0.59	0.44
Forbs	20 (0.68)	15 (0.64)	16.18	< 0.01
Shrubs	12 (1.00)	12 (0.76)	0.52	0.47
Rock	18 (0.98)	15 (0.94)	8.30	< 0.01
Log	9 (0.48)	12 (0.44)	12.39	< 0.01
Water	7 (0.52)	1 (0.25)	79.59	< 0.01
Slope aspect (%)			Z = - 3.59	< 0.01
North	19%	32%		
East	31%	26%		
South	33%	22%		
West	17%	20%		
No. burrows in 4-m radius	1.6 (0.13)	0.9 (0.09)	Z = - 7.14	< 0.01
No. shelters in 4-m radius	3.5 (0.27)	1.9 (0.16)	Z = - 7.97	< 0.01

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

TABLE 4. Characteristics of 26 over-wintering sites of Western Toads in five study areas in northeastern Oregon, 2002-2004.

	STUDY AREA					
Variable	**Balm**	**Twin**	**Fish**	**Crawfish**	**Lilypad**	**Total**
Elevation (m)	1368	1944	1992	2094	2130	
No. toads	7	5	9	1	4	26
Males (%)	29%	60%	33%	100%	100%	50%
Mean distance to site from breeding site (m) (range)	4063 (2028-6230)	982 (180-2220)	1694 (50-3440)	540	510 (240-920)	1968 (50-6230)
Type of site						
Burrow	86%	20%	22%	0%	25%	38%
Rock	0%	20%	56%	0%	25%	27%
Log/roots	14%	20%	22%	0%	25%	19%
Bank	0%	40%	0%	100%	25%	15%

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.

Class/Order/Family	**Prey items (*N*)**	**Samples with prey item (*N*)**	**% by order**
Insecta		91	
Hymenoptera (ants, bees, and wasps)		83	81.9
Formicidae (ants)	439	45	
Formica (Formica ants)	625	48	-
Camponotus (carpenter ants)	429	49	-
Vespidae (wasps)	7	6	
Other	11	7	-
Coleoptera (beetles)		57	12.6
Carabidae (ground beetles)	67	23	-
Staphylinidae (rove beetles)	23	8	-
Curculionidae (snout beetles)	13	11	-
Scarabaeidae (scarab beetles)	6	3	-
Other (>6 families)	124	39	-
Diptera (flies) (>1 family)	16	10	0.9
Orthoptera (grasshoppers)	8	6	0.4
Lepidoptera (butterflies and moths)	7	6	0.4
Heteroptera (true bugs) (>2 families)	8	6	0.2
Trichoptera (caddisflies)	6	4	0.3
Dermaptera (earwigs)	5	1	0.3
Homoptera (hoppers, aphids)	1	1	0.1
Plecoptera (stoneflies)	1	1	0.1
Arachinida (arachnids)		30	2.2
Araneae (spiders)	25	23	-
Opiliones (harvestmen)	11	9	-
Acari (mites and ticks)	5	2	-
Chilopoda (centipedes)	4	3	0.2
Diplopoda (millipedes)	3	1	0.2

FIGURE 4. Western Toads used the rocky habitat in the foreground for summer habitat and the wet meadow for breeding in the spring. The adjacent landscape had been burned by a wildfire.

in Colorado (Muths 2003), 1.9 in Idaho (Bartelt et al. 2004), and 2.6 in this study.

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 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).

Refugia may contribute to thermal regulation, moisture retention, and protection from predators (Schwarzkopf and Alford 1996). These habitat characteristics were not common in these study areas, and they became scarcer over the summer when intermittent streams and seeps dried. In this study, a second radio-tagged toad or an unmarked toad was found frequently within 20 m of the target animal. Because Western Toads are solitary beyond the breeding season (Loeffler 2001), this observation suggests that these particular habitats are being sought out. Multiple animals were found at certain locations, even at great distances from the breeding sites (Fig. 1, 2).

The majority (70%) of hibernacula I found did not have water nearby, which is in contrast to Campbell's (1970a) finding that hibernacula need a continuous flow of ground water beneath the chamber to prevent toads from freezing. 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, *Dytiscus*) were found in 15 toad stomachs in Colorado (Burger and Bragg 1947).

Disturbance.—The effects of disturbance events on toads are largely unknown. Although the sample size is limited, habitat alteration due to wildfires at Fish, Twin, and Crayfish did not appear to be detrimental to toads. Habitats with stand replacement 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.

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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, Eremais 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

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 gracea*, 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*

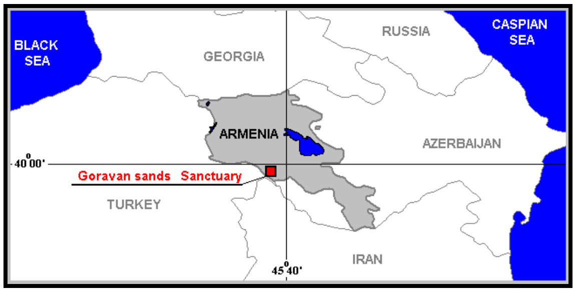


FIGURE 1. Geographic location of The Goravan Sands Sanctuary in Armenia.

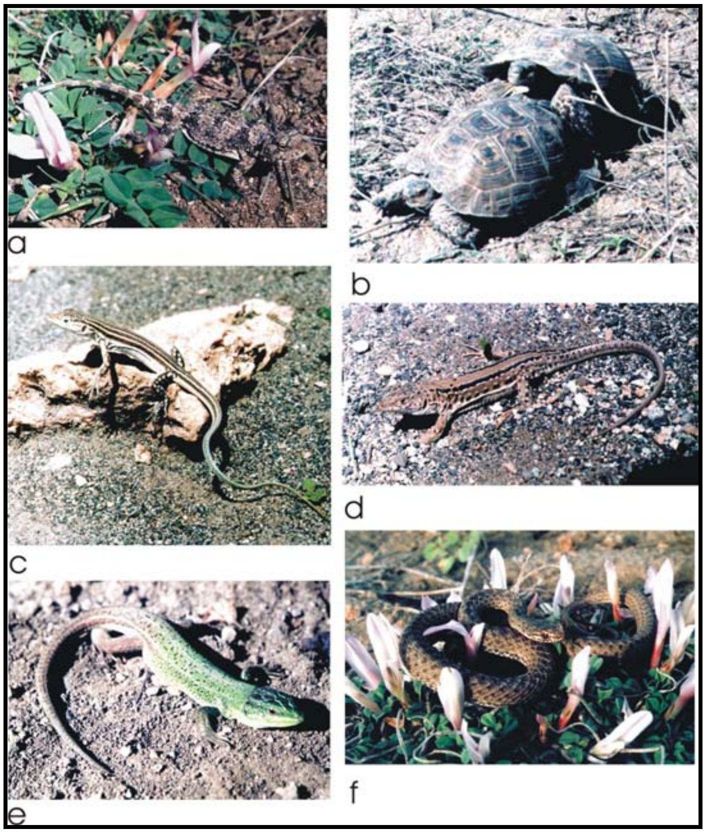


FIGURE 2. Representative photographs of reptiles from the Goravan Sands Sanctuary, Armenia: (a) Persian Toad-headed Lizard *Phrynocephalus persicus*; (b) Mediterranean Tortoise *Testudo graeca*; (c) Pleske's Racerunner *Eremias pleskei*; (d) Shtraukh's Racerunner *Eremias strauchi*; (e) Striped Lizard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

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 (N_2), and relative abundance of species (%). E = *East;* N = *North;* N_2 = *Hill's species diversity index.*

Quadrats			Species Diversity and Density (Specimens/Quadrat)					
N/N	E (d.ddddd)	N (d.ddddd)	*P. persicus*	*E. strauchi*	*E. pleskei*	*L. strigata*	*T. graeca*	(N_2)
1	39.88825084	44.73345295	0	3	0	0	0	0.11
2	39.89191068	44.71955300	0	6	0	0	0	0.03
3	39.89224085	44.73402286	0	2	0	0	0	0.25
4	39.89395067	44.71841297	1	0	0	0	0	1.00
5	39.89259065	44.71697301	0	0	5	0	0	0.04
6	39.89013065	44.71682306	0	1	2	0	0	0.11
7	39.89673067	44.71835292	0	0	6	0	0	0.03
8	39.89227063	44.71555303	0	0	2	0	0	0.25
9	39.89348087	44.73554282	0	0	4	0	0	0.06
10	39.89195075	44.72559295	0	0	3	0	0	0.11
11	39.89190062	44.71445305	1	3	0	0	0	0.06
12	39.89226063	44.71554303	0	3	0	0	0	0.11
13	39.89775068	44.71928289	0	0	0	1	0	1.00
14	39.89490072	44.72325291	0	0	6	0	0	0.03
15	39.89194077	44.72717293	0	0	2	0	1	0.1
16	39.89426073	44.72416291	0	4	0	0	0	0.06
17	39.89433081	44.73069285	2	0	5	0	0	0.02
18	39.89134059	44.71158309	1	0	7	0	0	0.02
19	39.89112054	44.70803312	0	0	1	0	0	1.00
20	39.89423066	44.71764297	1	0	0	0	0	1.00
21	39.89263671	44.71141518	2	0	0	0	0	0.25
22	39.89400063	44.71494300	1	1	0	0	0	0.25
23	39.89572069	44.72029292	0	1	0	0	0	1.00
24	39.89537063	44.71533297	0	0	0	0	0	-
25	39.88797087	44.73573293	1	0	1	0	0	0.25
26	39.89136064	44.71615304	0	1	4	0	0	0.04
27	39.89182079	44.72881292	4	0	1	0	0	0.04
28	39.89657064	44.71623294	0	0	0	0	0	-
29	39.89254077	44.72693292	1	1	8	0	0	0.01
30	39.89244082	44.73141288	0	0	7	0	0	0.02
31	39.88870085	44.73401293	0	0	4	0	0	0.06
32	39.89378081	44.73042287	0	0	2	0	0	0.25
33	39.89677066	44.71743293	0	0	0	0	0	-
34	39.89521080	44.73002284	1	0	0	0	0	1.00
35	39.89117056	44.70953311	0	0	0	0	0	-
Specimens/Relative abundance (%)			16/<14	26/<23	70 /<61	1/<1	1/<1	
Total			114 (100%) of individuals					

monspessulanus, Fig. 2f).

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).

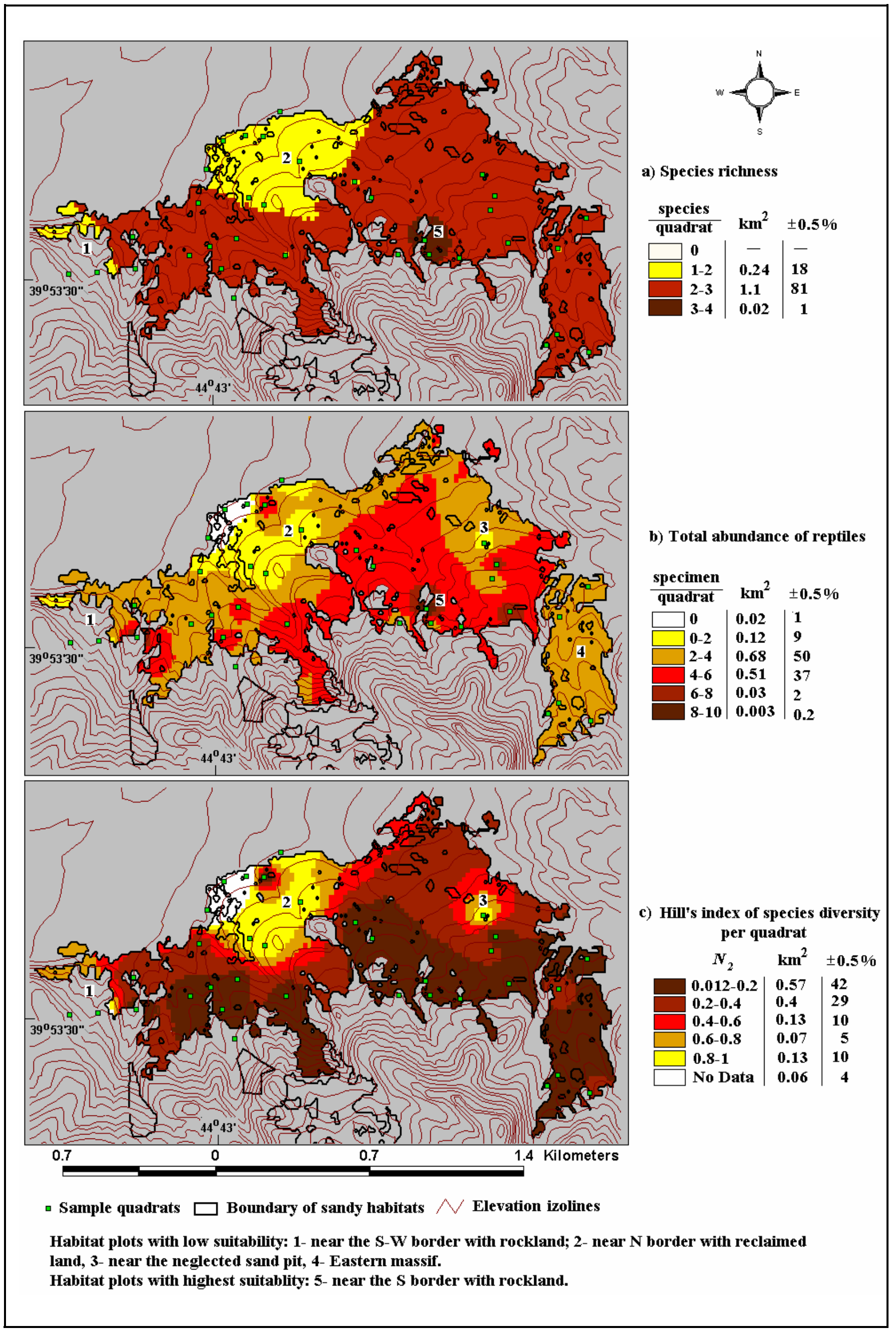
We surveyed quadrats once in randomized order between 1000-1800 hrs in March-June 2005. I recorded the point coordinates of the search areas using the GPS unit. Capture was used to identify individuals. Specimens were captured and individually marked on the ventrum with a felt tip marker and then released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



Habitat plots with low suitability: 1- near the S-W border with rockland; 2- near N border with reclaimed land, 3- near the neglected sand pit, 4- Eastern massif.
Habitat plots with highest suitablity: 5- near the S border with rockland.

FIGURE 3. Interpolated maps a) Species richness, b) Total abundance of reptiles, c) Hill's (N_2) index of species diversity. (Fig. 1).

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.

TABLE 2. Significance of Differences Among Mean Abundance of Species. Significant *p*-levels of Fisher's LSD test are bolded.

Taxon (mean abundance)	*E. pleskei*	*E. strauchi*	*P. persicus*	*L. strigata*	*T. graeca*
E. pleskei (*n* = 35; *M* ± *SE* = 2 ± 0.144; *R* – 0-8)	-	**<0.001**	**<0.001**	**<0.001**	**<0.001**
E. strauchi (*n* = 35; *M* ± *SE* = 0.743 ± 0.24; *R* – 0-6)	**<0.001**	-	0.38	**<0.001**	**<0.001**
P. persicus (*n* = 35; *M* ± *SE* = 0.457 ± 0.14; *R* – 0-4)	**<0.001**	0.38	-	0.19	0.19
L. strigata (*n* = 35; *M* ± *SE* = 0.0286 ± 0.029; *R* – 0-1)	**<0.001**	**<0.03**	0.19	-	1.00
T. graeca (*n* = 35; *M* ± *SE* = 0.0286 ± 0.029; *R* – 0-1)	**<0.001**	**<0.03**	0.19	1.00	-

Maps of species richness (Fig. 3a), total reptile abundance (Fig. 3b) and Hill's (N_2) 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_2), 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 abundance of reptiles, relatively low abundance for the Eastern massifs of sandy habitats (Fig. 3b: 4) and the plot with highest abundance (Fig. 3b: 5). The map of N_2 (Fig. 3c) illustrates the three plots with low species diversity, excluding plot 5, which had the highest diversity.

DISCUSSION

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 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_2. 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 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_2) at the Gorvan Sands Sanctuary, Armenia.

Variables	*P. persicus*	*E. strauchi*	*E. pleskei*	*L. strigata*	*T. graeca*	Numbers of Species	Total abundance	Hill's N_2 index
P. persicus	1.00	-0.11; p = 0.5 n = 35	-0.04; p = 0.82	-0.11; p = 0.51 n = 35	-0.11; p = 0.51 n = 35	**0.53;** **p<0.01**	0.13; p = 0.45	-0.002; p = 0.99
E. strauchi	-0.11; p = 0.5 n = 35	1.00	-0.33 p = 0.5	-0.11 p = 0.52 n = 35	-0.11 p = 0.52 n = 35	0.26 p = 0.14 n = 35	0.22 p = 0.21 n = 35	-0.11 p = 0.57 n = 31
E. pleskei	-0.04; p = 0.82 n = 35	-0.33 p = 0.56 n = 35	1.00	-0.16 p = 0.35 n = 35	0.08 p = 0.64 n = 35	**0.42** **p < 0.05** **n = 35**	**0.73** **p < 0.0001** **n = 35**	**-0.71** **p < 0.0001** **n = 31**
L. strigata	-0.11; p = 0.51 n = 35	-0.11 p = 0.52 n = 35	-0.16 p = 0.35	1.00	-0.03 p = 0.87 n = 35	-0.06 p = 0.74 n = 35	-0.18 p = 0.3 n = 35	0.26 p = 0.16 n = 31
T. graeca	-0.11; p = 0.51 n = 35	-0.11 p = 0.52 n = 35	0.08 p = 0.64	-0.03 p = 0.87 n = 35	1.00	0.23 p = 0.18 n = 35	0.02 p = 0.92 n = 35	0.02 p = 0.91 n = 31
Species Richness	**0.53;** **p < 0.01** **n = 35**	0.26 p = 0.14 n = 35	**0.42** **p < 0.05** **n = 35**	-0.06 p = 0.74 n = 35	0.23 p = 0.18 n = 35	1.00	**0.59** **p < 0.001** **n = 35**	**-0.37** **p < 0.05** **n = 31**
Total abundance	0.13; p = 0.45 n = 35	0.22 p = 0.21 n = 35	**0.73** **p < 0.0001** **n = 35**	-0.18 p = 0.3 n = 35	0.02 p = 0.92 n = 35	**0.59** **p < 0.001** **n = 35**	1.00	**-1.00** **n = 31**
N_2 index	-0.002; p = 0.99 n = 31	-0.11 p = 0.57 n = 31	**-0.71** **p < 0.0001** **n = 31**	0.26 p = 0.16 n = 31	0.02 p = 0.91 n = 31	**-0.37** **p < 0.05** **n = 31**	**-1.00** **n = 31**	1.00

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 multicolinearity in to analyses and confound regression analysis. In general, patches of high and moderate diversity (N_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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STATUS AND GEOGRAPHIC EXPANSION OF THE MEDITERRANEAN GECKO, *HEMIDACTYLUS TURCICUS*, IN LOUISIANA: IMPLICATIONS FOR THE SOUTHEASTERN UNITED STATES

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***Abstract.*—We used literature records, unpublished museum records, and unvouchered reports to evaluate the status of the Mediterranean gecko (*Hemidactylus turcicus*) in Louisiana since its last comprehensive treatment in 1989. During the last 17 years, the known geographic range of this species has expanded from four to 30 parishes following a pattern that is commensurate with extensive human-mediated dispersal. Its strong association with, and use patterns of, buildings in Louisiana are similar to those of the species elsewhere. Potentially limiting competitors and predators have not been identified in urban settings. Potential for competition with hylid treefrogs in ruderal settings remains unresolved, and in many urban settings the potential for syntopy is low. Louisiana and the southeastern United States in general are amenable to colonization by *H. turcicus* with the northern edge of its geographic range being dictated by climate. However, the future status of this species within the southeastern United States will be strongly influenced by the thermal tolerances of a suite of recent and competitively superior gecko species that displace this species in Texas and Florida.**

Key Words.—exotic species; *Hemidactylus turcicus*; invasive species; Mediterranean Gecko

INTRODUCTION

Exotic species constitute a global issue (Mooney and Hobbs 2000; Van Driesche and Van Driesche 2000) of which 276 species are amphibians and reptiles (Lever 2003; Meshaka et al. 2004; Meshaka 2006). Using the criteria of Meshaka and colleagues (2004), 48 exotic species of amphibians and reptiles are established in the southeastern United States (Conant and Collins 1998; Ferner and Ferner 2002; Lever 2003; Hardy 2004; Meshaka et al. 2004; Wallace 2005; Meshaka 2006). In the southeastern United States, the Mediterranean Gecko (*Hemidactylus turcicus*) occurs in Alabama (Conant and Collins 1998), Arkansas (Paulissen and Buchanan 1990, 1991; White and Tumlison 1999; Manning and Briggler 2003; Sheehy 2004; Trauth et al. 2004), Florida (Conant and Collins 1998; Johnson et al. 2002; McCoid 2002; Townsend et al. 2002; Townsend and Krysko 2003; Meshaka et al. 2004; Krysko et al. 2005), Georgia (Mills 1990; Frick 1997; Conant and Collins 1998), Louisiana (Dundee and Rossman 1989; Conant and Collins 1998), Mississippi (Conant and Collins 1998), South Carolina (Eason et al. 2000), and (for eastern) Texas (Conant and Collins 1998; Malone 1998; Saenz 1998; McAllister and Welsh 2001; McAllister 2004). This species is also possibly established in Virginia (Kleopfer et al. 2006).

Hemidactylus turcicus is also the oldest of four species comprising the exotic herpetofauna of Louisiana: the Greenhouse Frog (*Eleutherodactylus planirostris*) (Dundee and Rossman 1989), the Brahminy Blind Snake (*Ramphotyphlops braminus*) (Thomas 1994), and the Rio Grande Chirping Frog (*Syrrhophus cystignathoides*) (Hardy 2004). Like *E. planirostris*, present in New Orleans Parish since 1975 (Plotkin and Atkinson 1979), *H. turcicus* was believed to be present in the same parish since the 1940s (Etheridge 1952; Viosca 1957); its colony, likewise, was thought to be derived from trade along the Mississippi River (Etheridge 1952). Since the work of Dundee and Rossman (1989), *H. turcicus* has been reported elsewhere in Louisiana (Jensen and George 1993; Vidrine and Hatler 1995; Boundy 1994; Burke 1996; Watkins-Colwell et al. 1996; Ray and Cochran 1997; Williams 1997; Boundy 2004; Hardy et al. 2005).

Our objectives are to summarize the status and colonization dynamics of *H. turcicus* in Louisiana and relate our findings to the colonization patterns of this species elsewhere in the Southeast and more generally to ecological correlates of colonization success noted in other species (Mayr 1965; Brown 1989; Ehrlich 1989; Pimm 1989).

MATERIALS AND METHODS

We examined historical records (following Dundee and Rossman 1989), published records since Dundee and Rossman (1989), unpublished museum records, and reports (reliable observations) of *H. turcicus* in Louisiana through April 2006. We used the locality data to produce a geographic distribution map for Louisiana (Fig. 1). During 14-16 October 2005, two of us (WEM and SDM) conducted a nighttime survey of buildings centered in the immediate vicinity of 300 South Drive, Natchitoches, Natchitoches Parish, Louisiana. We deposited all specimens of *H. turcicus* collected for this study in the vertebrate collection of Northwestern State University in Natchitoches.

RESULTS AND DISCUSSION

***Temporal and spatial patterns of dispersal.*—**Since the first summary (Dundee and Rossman 1989), 13 new records (Jensen and George 1993; Vidrine and Hatler 1995; Boundy 1994; Burke 1996; Ray and Cochran 1997; Williams 1997; Boundy 2004;

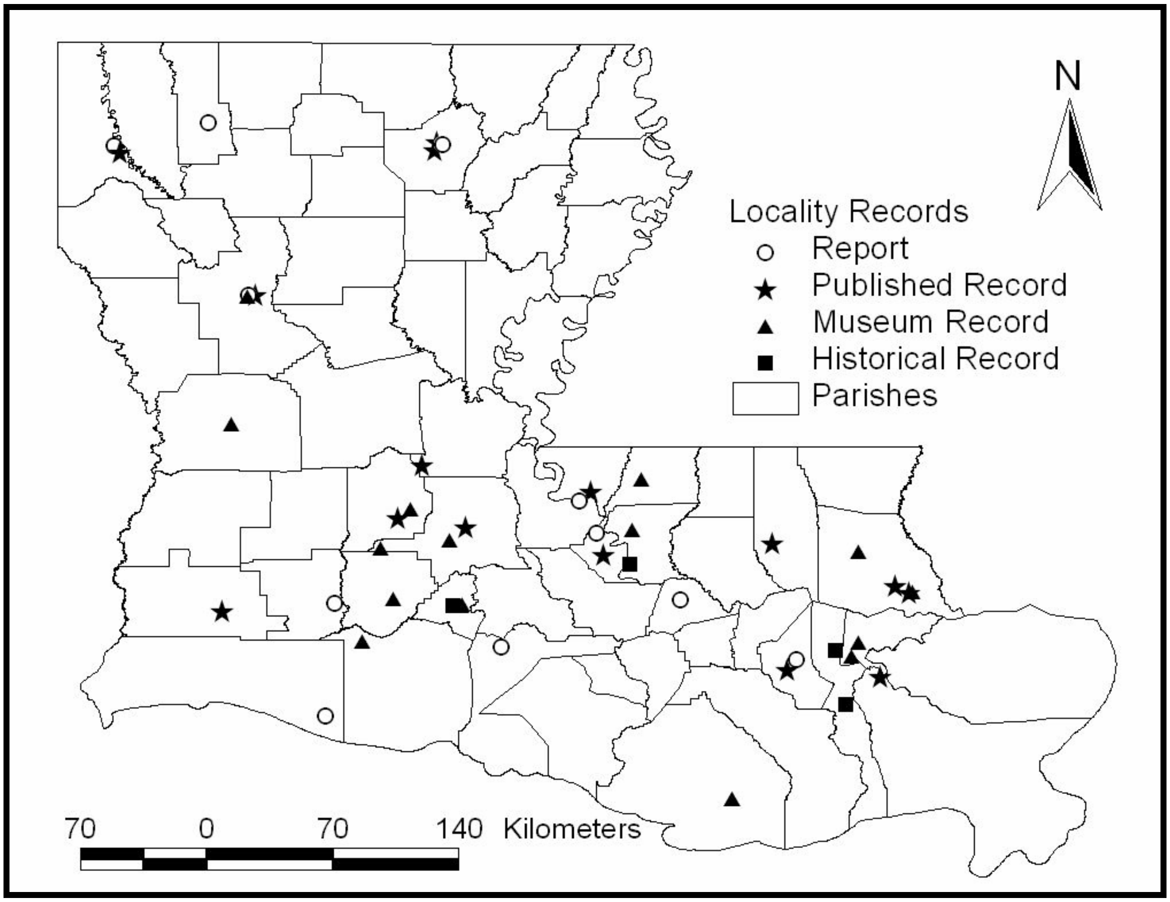

FIGURE 1. Geographic distribution of the Mediterranean gecko (*Hemidactylus turcicus*) in Louisiana.

Hardy et al. 2005) and one duplicate record (Watkins-Colwell et al. 1996) have been published on the distribution of *H. turcicus* in Louisiana. All records were published within 12 years of each other (1993-2005), and captures ranged over a 38-year span (1963-2001) suggesting colony ages were noticeably older than the initial captures from the 1990s.

The spatial disparity of museum records (we include LSUMZ 14166, 45974, 56767, 57657, 59593, 80354; LSUE 0044, 0069, 0331, 0646, 0961, 1021, 1258, 1475, 2163, 2319) and reports suggests an even greater geographic distribution than revealed by our map (Fig.1). Elsewhere in the United States, *H. turcicus* has a scattered geographic distribution often attributed to human-mediated dispersal (Conant and Collins 1998; Meshaka et al. 2004; Trauth et al. 2004). Some of the earliest known records are from port cities, such as Key West (Fowler 1915), New Orleans (Etheridge 1952), and Brownsville (Conant 1955). Many records, including those here, are associated with cities and universities (Davis 1974; Mount 1975; Marion and Bosworth 1982; Selcer 1986; Nelson and Carey 1993; Punzo 2001a; Meshaka et al. 2004; Trauth et al. 2004). These sites also offer the likelihood of intentional—examples have been observed by one of us (Jeff Boundy)—and unintentional human-mediated dispersal. In Louisiana, sites such as Shreveport and Natchitoches to the north, Alexandria in the central region, and Lake Charles, Lafayette, and New Orleans to the south are trade routes that could easily serve as intrastate sources of gecko colonies as well as eventual two-way sources of colonies most readily with east Texas. In this connection, the northward dispersal of *H. turcicus* from Brownsville, Texas, followed major highways with produce trucks being the likeliest dispersal agents (Davis 1974). In south-central Florida, *H. turcicus* colonies also followed major trucking routes (Meshaka 1995). More specifically, Selcer (1986) thought that because of low individual vagility, a trait also noted in Louisiana (Rose and Barbour 1968) and Florida (Punzo 2001), eggs were the more likely life cycle stage to be transported incidentally by humans.

High vagility is a correlate of successful colonization (Ehrlich 1989). For *H. turcicus*, a high rate of human-mediated dispersal is responsible for the rapid and scattershot dispersal pattern of this species in Louisiana and elsewhere with each new colony increasing the likelihood of future dispersal events.

Habitat preference.—Successful dispersal of *H. turcicus* to Louisiana cities is due to its strong association with buildings (Rose and Barbour 1968; Dundee and Rossman 1989). In all but one subsequent Louisiana distribution record for which habitat is described, *H. turcicus* is associated with buildings. Unlike the other sites, the St. Charles Parish record (Boundy 2004) was associated with construction debris that had been dumped in a swamp. In Louisiana, we saw individuals mostly on buildings, especially those made of brick or cement. Wood sidings of such buildings are also used. One of us (Jeff Boundy) observed two exceptions: (1) juvenile individuals at dusk on sidewalks located more than 10 m from houses; and (2) six adults captured from a

TABLE 1. Relative abundances of the Mediterranean Gecko (*Hemidactylus turcicus*) observed at selected sites in the southern United States.

Location	Observations (Geckos/Min)	Source
Alabama		
Fairhope	0.13	(Nelson and Carey, 1993)
Mobile	0.08	(Nelson and Carey, 1993)
Florida		
Panama City	0.03	(Nelson and Carey, 1993)
Pensacola	0.08	(Nelson and Carey, 1993)
Louisiana		
New Orleans	7.2	(Dundee and Rossman, 1989)
Natchitoches	0.6	(This study 15 Oct 2005)
Natchitoches	0.8	(This study 16 Oct 2005)
Mississippi		
Gulfport	0.05	(Nelson and Carey, 1993)
Texas		
Edinburg	0.21	(Selcer, 1986)

dead pecan tree in a large mowed area ca. 33 m from brick buildings. Rose and Barbour (1968) also observed juveniles on sidewalks. A nearly exclusive association with buildings, especially those associated with rough surfaces (Nelson and Carey 1993), has also been noted elsewhere in the United States (Paulissen and Buchanan 1991; Meshaka 1995; Punzo 2001a; Meshaka et al. 2004).

Hemidactylus turcicus populations in Natchitoches, as elsewhere (Table 1; Selcer 1986; Punzo 2001a; Hibbs et al. 2004) vary widely in size and can be exceedingly dense. Preferred habitat in the southeastern United States is a combination of masonry buildings with dim incandescent lighting (Nelson and Carey 1993). Such might be the case in stone masonry crypts of cemeteries favored by this species in New Orleans (Rose and Barbour 1968). Differences in population size, thought to be affected by prey abundance, are also associated with differences in body length and condition of the geckos (Hibbs et al. 2004). In turn, spiders, roaches, and crickets (Nelson and Carey 1993) and, more specifically nocturnal wolf spiders and crab spiders (Punzo 2005), decline in the presence of *H. turcicus*.

Coexistence with humans is a correlate of colonization success (Brown 1989). For *H. turcicus*, a close association with human-made structures has provided it with an abundance of potentially high quality habitat in Louisiana and elsewhere in the southeastern United States that simultaneously functions as sources for further dispersal.

Potential competitors.—During our searches in Natchitoches, all individuals we encountered were in areas away from non-incandescent lights, a phenomenon also noted by Nelson and Carey (1993). The species avoids direct light, favoring partial light and darkness (Paulissen and Buchanan 1991; Nelson and Carey 1993). Likewise, we found individuals not only in dark areas but not in even peripherally-lighted areas that could provide superior sources of insect prey. This behavioral limitation is absent in its superior competitive congeners, the Indo-Pacific Gecko (*Hemidactylus garnotii*) and the Wood Slave (*Hemidactylus mabouia*) in Florida (Meshaka et al. 2004), each with differential colonization traits (Punzo 2005). Although the mechanisms for its replacement by *H. garnotii* and *H. mabouia* in Florida are unknown (Meshaka et al. 2004), *H. turcicus* is socially dominated by *H. garnotii* (Frankenburg 1984) and has a lower fecundity and narrower habitat range than its two congeners (Meshaka et al. 2004 and citations therein). Also, digestive and assimilation efficiencies and the rate of its gastric evacuation in *H. turcicus* are lower than those of *H. mabouia* (Punzo 2001b). Perhaps, the aversion of *H. turcicus* to bright incandescent lights and non-incandescent lights (e.g., fluorescent and orange sodium vapor lights) (Nelson and Carey 1993; this study), even when alone, may be added to the list of disadvantages contributing to its sharp decline in Florida.

The species is a dietary generalist in Florida (Punzo 2001a; Meshaka et al. 2004), Louisiana (Rose and Barbour 1968), and Texas (Saenz 1996). Its diet varies seasonally (Rose and Barbour 1968) and spatially on building walls (Saenz 1996). However, in Texas, it is replaced by the Roughtail Gecko (*Cyrtodactylus scaber*), concomitant with behavioral (Vaughan et al. 1996) and dietary shifts (Klawinski et al. 1994). Urban settings often have many poorly occupied niches decreasing the opportunities for competition between hylids and geckos. The potential for food competition between *H. turcicus* and arboreal hylids in this setting where syntopy is possible in Louisiana as well as in ruderal settings remains an unresolved topic. In southern Florida, dietary overlap is high between the Green Treefrog (*Hyla cinerea*) and the Squirrel Treefrog (*H. squirella*); whereas, dietary overlap ranges from low to intermediate between the treefrogs and two syntopic hemidactyline gecko species (Meshaka 2001). Open niche space is a correlate of successful colonization (Brown 1989). For *H. turcicus*, this correlate appears to be met in Louisiana; however, in Florida and Texas this species is gradually being displaced by other exotic geckos.

Predators.—No reported limiting predators of *H. turcicus* are known in Louisiana. In Florida, it is preyed upon by spiders, whip scorpions, cats, bats, and Cuban Treefrogs (*Osteopilus septentrionalis*) (Punzo 2001a). Yet, even under those circumstances, population densities of *H. turcicus* can still be high (Punzo 2001a). In Natchitoches, Louisiana, we observed none of the adults near the ground. Similarly, adults in Florida are generally found higher on walls and also found in the vicinity of refuges more often than subadults (Gomez-Zlatar and Moulton 2005). Subadults and juveniles were preyed on by cats when ascending buildings in the evening and at normal foraging times, subadults and adults are generally within 33 cm of porch ceilings (Jeff Boundy, pers. obs.). In Arkansas, most individuals were found higher than 4.5 m above the ground (Paulissen and Buchanan 1991). Predator-free space is a correlate of successful colonization (Pimm 1989). For *H. turcicus*, predators are not as well documented in Louisiana as they are elsewhere and truly limiting predators of this species do not yet appear to have been identified. Like *O. septentrionalis* in Florida (Meshaka 2001), *H. turcicus* in Louisiana might be relatively free of predators in some places and able to flourish in other places even with a suite of predators that also eat one another and do not specialize in eating this small nocturnal vertebrate.

Cold tolerance.—Louisiana populations are active in ambient temperatures as low as 3.3^{o} C (Rose and Barbour 1968; Dundee and Rossman 1989.). This ability, combined with the thermal inertia associated with brick and concrete buildings may allow colonies to persist in northern Louisiana (this study), in northern Arkansas (Paulissen and Buchanan 1991; Trauth et al. 2004) and central Oklahoma (Conant and Collins 1998). The cost, at least in northwest Arkansas as compared to more southerly populations (Rose and Barbour 1968; Selcer 1986; Meshaka 1995; Punzo 2001a), is an abbreviated egg-laying season and more seasonal limitations to foraging activity on the exterior of buildings where most individuals were seen (Paulissen and Buchanan 1991). Thus, in the southeastern United States, especially in lower elevations, climate provides a weak constraint to the colonization of *H. turcicus*. Ultimately, however, colder climate farther north will determine the northern distributional range of this species at a point where not enough time is available for breeding or foraging. Tolerance of a wide range of physical conditions is a correlate of successful colonization (Mayr 1965). For *H. turcicus*, the ability to function across a wide thermal gradient has contributed to its northern expansion in Louisiana and the southeastern United States in general.

Our study corroborated several characteristics of Louisiana *H. turcicus*: High vagility in the agency of humans, near exclusive association with buildings or building materials, an apparent open niche space in urban areas, potentially predator-free in some areas, and the ability to remain active at low ambient temperatures. These aforementioned characteristics conform to predictions of successful colonization. Rapid dispersal over wide areas and the potentially high abundance of *H. turcicus* are measures of its colonization success both in Louisiana and elsewhere in the southeastern United States. However, as this species has been replaced by recently introduced competitively superior geckoes in Texas and Florida, in addition to climate, its geographic distribution in the southeastern United States will be affected by the ultimate range expansion of its competitors. In this regard, *H. turcicus* could potentially be extirpated from the southeastern United States if its thermal tolerances are exceeded by those of its competitors.

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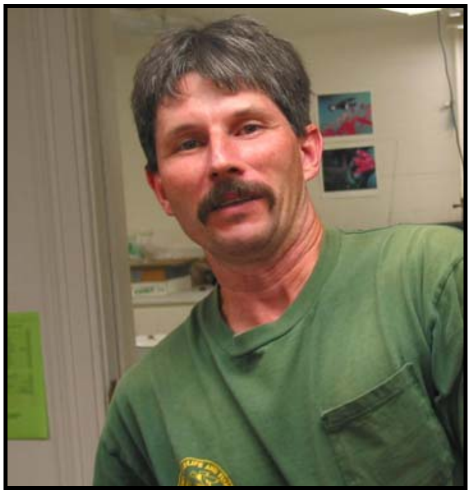

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A NOVEL FACULTATIVE MUTUALISTIC RELATIONSHIP BETWEEN BUFONID TADPOLES AND FLAGELLATED GREEN ALGAE

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***Abstract*.—Variable environments can produce intolerable conditions for certain species. In some cases, survival is assured by fortuitous mutualistic interactions. We show that the critical thermal maximum (CTM) for *Bufo* tadpoles is increased when the green alga *Chlorogonium* aggregates on their skins in warm ephemeral pools. The congregation of *Chlorogonium* may have been a response toward a source of otherwise limiting CO_2, reciprocally providing O_2 to the stressed tadpoles. Such a relationship has not been reported previously for these organisms.**

Key words.— *Bufo; Chlorogonium*; mutualism; symbiosis; tadpole; toad

INTRODUCTION

Many ecologically important mutualisms are conditional and occur because they provide partner species with novel options for adjusting to changing environments (Hay 2004). For example, organisms reaching their critical thermal maximum (CTM) (Hutchison 1961) are incapable of escaping the lethal conditions. Aquatic organisms in thermally uniform systems have no refuge from heat stress; further, temperature increases within such systems decreases the concentration of the necessary gases oxygen (O_2) and carbon dioxide (CO_2) (Randall 1997). Aquatic organisms that are stressed for these gases for respiration and photosynthesis would benefit from fortuitous mutualistic interactions in which the "by-product" gases evolved by metabolism can be absorbed reciprocally (Hay 2004; Connor 1995).

A field observation allowed us to evaluate a hypothesis of such a fortuitous mutualistic interaction. We discovered numerous tadpoles of the Dwarf American Toad (*Bufo americanus charlesmithi*) in a shallow temporary pool subjected to extended exposure to solar radiation. The water became very warm by mid-afternoon, and some of the tadpoles possessed an atypical greenish coloration (Fig. 1). The tadpoles were late stage, and some of them exhibited well-developed legs. The pool, located in ruts of a logging road near Crossett, Ashley County, Arkansas, USA, was examined from 5-10 June 2000. Microscopic examination (60X) of live tadpoles from the pool revealed clusters of biflagellated green organisms, identified as *Chlorogonium*, scattered as greenish blotches over the skin. Individuals of this alga were observed actively flagellating to maintain a position oriented to the skin of the tadpole (Fig. 2). The distribution of *Chlorogonium* generally followed the pattern of cutaneous blood vessels on the dorsal surfaces of the legs, tail, and lateral body wall.

Rates of cellular processes are temperature dependent (Q_{10} effects) to maximal values between 25-40^{o}C; therefore, CO_2 uptake from warmer water may occur faster than atmospheric replenishment and cause carbon depletion (Reynolds 1984). In consideration of the warmth of the pool and the likely stresses faced by both organisms, we hypothesized that the algae and tadpoles were in a relationship whereby metabolic gases evolved by each were being reciprocally absorbed.

Figure 1. Tadpoles of the Dwarf American Toad (*Bufo americanus charlesmithi*) with symbiotic algae visible as a green haze on the surface of the skin. Photograph by Stanley E. Trauth.

MATERIALS AND METHODS

If increased temperatures cause respiratory stress on tadpoles and coincidentally stresses algae starved for CO_2, a relationship beneficial to both organisms would be a reasonable strategy for the continued survival of each species. At the field site, temperatures were measured during the afternoon (after the ambient temperature peak), and observations were made on the behavior of tadpoles at that time. The ruts forming the pool produced four deeper areas located essentially in quadrants, with the northwest and southwest pools somewhat shaded during most of the morning and the northeast and southeast pools fully exposed to the sun to test the CTM of tadpoles without *Chlorogonium* as likely suppliers of O_2, we placed 30 tadpoles of normal grayish-brown coloration (with little or no *Chlorogonium*) into an aquarium containing a thermometer, mud substrate, and 3 cm depth of water (obtained from and simulating the pools). The aquarium then was exposed to direct sunlight to evaluate behavior of the tadpoles with increasing temperature. Behavior was observed in four separate trials of this experiment.

Figure 2. Scanning electron micrographs of *Chlorogonium* on the skin of tadpoles. Left photo shows a dense aggregation of *Chlorogonium* (scale bar = 10 µm); right photo shows an isolated individual (scale bar = 5 µm). Photomicrographs by S.E. Trauth.

In a separate experiment, 30 tadpoles with clearly evident and extensive patches of *Chlorogonium* were collected and placed into the same aquarium setup. The aquarium was positioned to be half in direct sun and half in shade to investigate behavior of the tadpoles within a thermally variable environment. Tadpoles initially were placed on the sunny side of the tank.

RESULTS

The deepest portion of any pool was 8 cm (southeast pool). On 7 June (1700 hr) the maximum temperature was 38°C, and all tadpoles showed normal flight responses to disturbance (a slow approach to within 1 m of the pools caused evasive behavior by the tadpoles.)

On 8 June (1430 hr), previously green tadpoles in the southwest pool had died when the temperature had reached 44°C. Those tadpoles no longer were green, indicating that the *Chlorogonium* had either died or had left the carcasses. Tadpoles in the better-shaded northwest pool behaved normally at 38°C, whereas those in the unshaded northeast pool were slower to move (i.e., a touch of the water was required to elicit evasive action). None of the tadpoles in this pool was dead or even exhibited difficulty with balance at 42.5°C. In the unshaded southeast pool at 41°C, the tadpoles moved only upon disturbance of the surface of the water. Moreover, in the southeast pool, a cluster of about 50 tadpoles scattered upon direct disturbance (tadpoles that were slowly touched), but they quickly returned to the 8 cm deepest portion of the pool.

In the aquarium experiment with brown tadpoles, normal behavior was observed up to a temperature of 38°C, but at 39°C a reduced flight response to approach was observed. At 39.5°C, tadpoles demonstrated difficulty with righting behavior, their locomotor activity appeared to be compromised, and their mobility was decreased. Some tadpoles appeared to be dying at this temperature, and death was certain at 40°C. Results were consistent in each of four replications of this experiment.

After water temperature in the insolated portion of the aquarium with green tadpoles had reached 40°C, just above the previously determined CTM temperature of 39.5°, only 18 of 30 individuals (60%) had adjusted their orientation into the shaded area, but at 44°C all tadpoles moved to the shaded microhabitat of the aquarium (36°C). Field observations already had shown that 44°C exceeded the critical maximum for tadpoles supported by a coat of ***Chlorogonium.***

DISCUSSION

Adult amphibians tend to seek temperatures within the range of 10-30°C (Brattstrom 1963), but tadpoles may develop more rapidly when in warmer temporary pools (for CTMs of various anuran larvae, see Ultsch et al. 1999). The high CTMs of toads help them survive in warmer conditions and shortens the time required for development, thereby promoting metamorphosis prior to desiccation of the habitat (Noland and Ultsch 1981). Tadpoles demonstrate plasticity in development rate (Tejedo and Reques 1994; see Altig and McDiarmid 1999) and can accelerate metamorphosis after detecting reduction of water volume (Denver et al. 1998).

Vernal pools exposed to direct sunlight and elevated temperatures promotes faster development of tolerant species such as toads (*Bufo* sp.) by increasing metabolic rate (Noland and Ultsch 1981) based on Q_{10} effects (Parker 1967; Ultsch et al. 1999; Gatten et al. 1992). The thermal optimum for locomotion in toads hypothetically evolved in response to selective pressures on juveniles (Tracy et al. 1993).

Rates of oxygen consumption in tadpoles increase with higher temperatures (Parker 1967; Marshall and Grigg 1980; Ultsch et al. 1999), but water at higher temperature holds a lower concentration of gases (Randall et al. 1997). Although tadpoles are tolerant to warmer temperatures, the O_2 deficits can lead to respiratory distress and death (see Ultsch et al. 1999). Under conditions of low O_2, tadpoles of some species can supplement oxygen intake by gulping air, but the late development of the lungs precludes this in *Bufo* (Duellman and Trueb 1994).

Consumption of O_2 increases sharply prior to metamorphosis (Feder 1982), thus the warmer water contains less O_2 at a time when more may be needed. Even after acclimation to warmer temperatures (Wilson et al. 2000), the CTM of tadpoles of most anuran species is 38-40°C (Duellman and Trueb 1994; Noland and Ultsch 1981), with a few exceptions above 41°C in species that develop in xeric or tropical habitats (Brown 1969).

The rate of photosynthesis tends to increase with increases in temperature up to an optimum temperature, after which it decreases rapidly, partly limited by the availability of inorganic carbon (Davison 1991). Growth rate of algae slows in stagnant cultures because the rate of diffusion of CO_2 from the air becomes limiting (Fogg 1975), partly because CO_2 diffuses 10^4X faster in air than in water (Graham and Wilcox 2000). The green algae (Chlorophyceae, including *Chlorogonium*) tend to dominate in temperatures of 15-30°C, but are replaced by blue-greens (Cyanobacteria) above 30°C (DeNicola 1996). Thermophilic algae thrive best in waters rich in CO_2, where conditions necessary for maintaining high rates of photosynthesis are met (Fogg 1969). We believe the pattern of association and distribution of *Chlorogonium* over the skin of tadpoles allowed maximum potential for uptake of otherwise limiting CO_2 released via cutaneous respiration by the tadpole.

The relatively small size of the *Chlorogonium* specimens also could indicate stress. The mean length of 103 individuals taken from the tadpoles was 13.4 µm (range 7-22), and width ranged only between 1.5-3 µm. The normal measurements from species known to occur in the United States ranges from 19-59 µm in length and 5-18 µm in width (Nozaki et al. 1998). Smaller cells result in a higher surface/volume ratio, which could help maximize absorption in a CO_2-limited environment (Foy 1980; Reynolds 1984).

A precedent for a mutualistic relationship between a flagellated green alga and amphibian larvae exists with *Oophila amblystomatis*, which is symbiotic within the egg jellies of spotted salamanders, *Ambystoma maculatum* (Gilbert 1942). The eggs of the salamander are surrounded by a gelatinous matrix, which impedes diffusion of O_2 toward the embryo and CO_2 from the embryo. *Oophila*, endogenous within the membranes of the eggs, absorbs the CO_2 produced during metabolism of the embryo, and the O_2 produced by the alga is available to the developing embryo (Pinder and Friet 1994). It has been argued that this arrangement leads to improved growth and survival of embryos due to decreased respiratory stress and enhances growth of the alga in a protective gelatinous medium.

Our experiments demonstrated that the CTM at which tadpoles of *Bufo americanus* could survive independently was 39.5°C. In a heat-stress-inducing environment, however, the CTM could be expanded by over 3°C (to about 43°) in the presence of a photosynthetic mutualist, such as *Chlorogonium*. Considering these phenomena, we hypothesize that the *Chlorogonium* and tadpoles were exhibiting a facultative symbiosis in which tadpoles gained O_2 produced via photosynthesis adjacent to the skin, and concomitantly the *Chlorogonium* received the metabolic CO_2 evolved from the tadpoles.

We suggest that future determinations of CTMs should consider factors in addition to temperature due to interactions. Although not investigated, we found similar algal accumulations on tadpoles of gray treefrogs (*Hyla versicolor*) and cricket frogs (*Acris crepitans*) at other locations within Arkansas.

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After the organizational meeting in Henderson, Nevada, participants spent the afternoon observing the wildlife and unique natural resources of Kelso Dunes in the Mohave National Preserve near Kelso, California, USA. Here, Roger Luckenbach, Ray Saumure, and Dave Germano look on as Stan Trauth Photographs an *Uma notata*. Kelso Dunes is among the largest sand dune areas in North America and the world. This area had been a haven for off road vehicle use, but efforts by ardent conservationists helped to make this area of scenic beauty and ecological importance off limits to vehicles. Photographed by Malcolm McCallum.

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NATURAL HISTORY, FIELD ECOLOGY, CONSERVATION BIOLOGY AND WILDLIFE MANAGEMENT: TIME TO CONNECT THE DOTS

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***Abstract*.—Natural history and field ecology are essential building blocks for successful conservation and management of herpetofauna. Thus, natural history and field ecology merit major infusions of funding and increased recognition of their importance in science and management. Others have stated matters well: (1) Academic training in natural history should receive high priority; (2) we need to integrate our work across disciplines (from molecules to communities), and use all of our knowledge toward common goals; (3) natural history is not dead but today is a flourishing enterprise; and (4) mutual respect and collaboration between disciplines best serve our own mental health as well as the future of natural history. We need to merge the best natural history, field ecological data, and biological questions with the latest advances in other fields of inquiry if we are to advance science and solve key environmental issues. It takes a scientific community and many concerned parties to save a species, let alone an ecosystem. We must connect these dots to see the big picture.**

Key words.—conservation, field biology, herpetology, natural history, wildlife management

INTRODUCTION

During the development of this inaugural issue of *Herpetological Conservation and Biology*, I wondered about several questions. Why start a new journal when some in our profession view collecting and reporting natural history or field biology information as unnecessary? What can we do collectively to organize our common goals to better understand the lives of amphibians and reptiles? Why are conservation efforts sometimes considered separate from scientific studies on the biology of amphibians and reptiles? How can we better protect and manage our dwindling herpetofauna? These questions are addressed here.

Recently, several authors expressed the importance and role of natural history and field biology in science (see Arnold 2003; Greene 2005; McCallum and McCallum 2006; Trauth 2006). Using their key points as a springboard, my specific objectives are to: (1) examine the general state of our thinking about the role of natural history and field biology in herpetology; (2) suggest ways to elevate these skills and tools to a more deserved level; (3) encourage studies from many disciplines and approaches to provide the best biology; and (4) recommend ways to link our common interests for improved conservation and management for our herpetofauna.

WORDS OF THE MASTERS

Most of the great biologists of our past and recent times were or are still "naturalists". A few outstanding examples are as follows:

Charles Darwin.—Instead of entering the seminary, Darwin went on worldly travels in his formative years. He collected animals and data in the wilds of South America and the Galapagos Islands, observed patterns in nature and thought about how all these happened. His naturalist start led him to be a proponent of evolutionary biology. Decades later these initial impressions resulted in his book, "*The Origin of Species…*" (Darwin 1859), where he stated at the outset:

"*WHEN on board H.M.S. Beagle, as naturalist, I was much struck with certain facts in the distribution of the inhabitants of South America, and in the geological relations of the present to the past inhabitants of that continent. These facts seemed to me to throw some light on the origin of species—that mystery of mysteries… On my return home, it occurred to me… that something might perhaps be made out on this question…*"

Aldo Leopold.—He wrote the first widely used book on wildlife biology (Leopold 1933), which made him the "father" of wildlife biology and management. As a professor at the University of Wisconsin, he spent breaks at a small cabin on land that served as a retreat. During this time, he was a naturalist (i.e., observer) and he became a deep thinker that led to his book "*A Sand County Almanac*" (Leopold 1949). This now serves as a major work of literature as well as inspiration to a generation of environmentalists (Flanders 1974, Meine 1988, Meine and Knight 1999).

Robert C. Stebbins.—He is often considered the dean of western herpetology and may be best known for his well-illustrated field guides (e.g., Stebbins 2003). These were based on detailed species accounts in earlier books (e.g., Stebbins 1962) and his years of field work. More recently, he co-authored a major book (Stebbins and Cohen 1995), where the authors state:

"Our selection of the title of the book, A Natural History of Amphibians, reflects our interest in individual animals and their populations, how and where they live and reproduce, how they interact with one another and their environment, and the evolutionary processes that have made them what they are and that continue to shape their future."

Further, they pointed out the decrease in teaching and research in natural history, but suggested it is equally important to other disciplines that we study life at the level of whole organisms and their interactions in nature.

Besides his fame as a natural historian, he conducted intensive scientific studies on a wide variety of topics: one of the first implants of a radio transmitter into a large Australian lizard (Stebbins and Barwick 1968), experimental removal of the parietal eye in Galapagos Islands lava lizards (Stebbins et al. 1967), function of the parietal eye (e.g., Eakin and Stebbins 1959), and speciation in the Ensatina, *Ensatina eschscholtzii* (Stebbins 1949, Brown and Stebbins 1964). He is a great educator and scientist with many interests and skills (e.g., he is an accomplished painter of African wildlife).

Eric Pianka.—When speaking as an invited lecturer to the International Congress of Zoology, Pianka (2002) stated that, "I fear that I must begin with some bad news for all zoologists: Zoology is rapidly becoming obsolete!" He compared a number of disciplines and noted that studies in areas like molecular biology deal with microscopic levels and data can be gathered relatively quickly, whereas fields like community ecology require lots of space and time to complete.

Further, he recognized that many scientists have been neglecting higher levels of organization (e.g., community ecology), which is worse than simple benign neglect because people working at each level (e.g., molecular, physiological) express disdain for those struggling to work at higher levels. He also pointed out that not only are "ology" courses (e.g., herpetology) disappearing from curricula everywhere, but also study of fields like molecular biology seldom provide great insights into the evolutionary forces that mold adaptations. He then stated that this thinking is perilous because all levels of approach are necessary to truly understand any biological phenomenon.

NATURAL HISTORY AND HERPETOLOGY: WHERE ART THOU TODAY?

Recently, I was talking with a professor in California and an undergraduate student (attending a nearby college). On her own, this student had started a field study to determine the occurrence of snakes at the San Joaquin Experimental Station (SJES) in central California. However, she was dismayed that her advisor said that "natural history was dead" and her time should be spent on a more fruitful line of inquiry. This attitude was insensitive for a professor to state as it discourages a student's interest in biology. Even in its narrowest definition (a descriptive study), a natural history study can be the impetus to interest students in biology or environmental issues. Interests in nature and wildlife may lead to employment focusing on conservation, applied ecology and wildlife management or to a rewarding career as a research scientist in academia or government.

Also, she selected an intriguing area and topic. Although Block et al. (1994) set 144 pitfall traps (18,780 trap days) at the SJES, they excluded snakes from all comparisons because they were not sampled adequately. Besides a SJES checklist (Newman and Duncan 1973), the student's study appears to be the first re-assessment of SJES snakes since Henry Fitch studies there six decades earlier (Fitch 1949, Fitch and Twining 1946). This is a valuable study because changes in species diversity, relative abundance, and community structure over time have intrinsic scientific value and conservation implications.

Far from its demise, natural history and field biology are alive and well (see Arnold 2003). There are many strong arguments in favor of field and natural history studies by many renowned biologists (Greene and Losos 1988; Noss 1996; Futuyma 1998). Also, natural history and field ecology do not have to be exclusive endeavors. Today, most biologists are engaged in varied multidisciplinary studies and conservation efforts. Natural history and field biology are part of our repertoire that we employ to solve questions (Fig. 1), particularly when dealing with conservation and management issues.

Further, it is myopic and erroneous to consider training as a naturalist as easy or some sort of outdoor play. Although field biologists know it, many other scientists would be aghast at the time, energy and endurance necessary to conduct field work (Pianka 2002). It is among the most demanding tasks mentally and physically. Studies in nature often appear 'messy' because there are many confounding environmental factors. Still, many of these complex questions require field-based approaches and demand our best minds to unravel their mysteries.

It is challenging to become an accomplished naturalist, field ecologist or wildlife biologist as one needs to learn not just the names and systematic status of plants and animals, but how to merge these data with distributional constraints, habitat associations, physiological constraints, and behavior of animals. Investigators in applied fields also must develop skills of persuasion to convince fellow humans to change their actions or work on coordinated efforts. Often, it is the naturalists or field ecologists who possess the broadest and deepest understanding of species in landscapes and ecosystems. They usually are the first to see the big picture.

This knowledge helps us to ask better experimental or theoretical questions. Experimental designs and tests usually focus on a few factors, and results can yield illuminating results and interpretations. Still, these studies are usually intensive and expensive to perform, which may limit their geographic scale or result in few replications. Further, modeling employs many factors with the latest technological prowess (computers), geographical information systems, and mathematical concepts. Many of these "data" or inputs, however, are suppositions or generalizations that have yet to be verified in the field. Modeling can summarize, display and interpret vast amounts of information, which is useful to answering many questions. However, sometimes models or computer simulations develop lives of their own not related to the field situation.

We need a balance or mutual respect for the contribution of all these fields and approaches to improve our understanding of species biology and community interactions. Each discipline may provide different interpretations, but multidisciplinary approaches can provide insights beyond that obtained via single endeavors. We need to use all of our knowledge to formulate the critical questions and employ collaboration from all quarters to best solve problems.

WHERE'S THE INFORMATION TO PROTECT SPECIES AND THEIR HABITATS?

Natural history or field ecological data are essential for effective protection and management of threatened and endangered species. For example, reliable information on many criteria (Table 1) is required for consideration on the International Union for Conservation of Nature's (IUCN) Red List of threatened species (http://www.iucnredlist.org/info/categories_criteria2001) (Mace and Lande 1991; Mace et al. 2002). The IUCN prefers a population viability analysis, which is a model that estimates the extinction probability of a taxon based on known life history, habitat requirements, threats and any specified management options. Few such analyses, however, exist for amphibians and reptiles.

The recent Global Amphibian Assessment (http://www.globalamphibians.org) (Stuart et al. 2004) included data on each of the 5,918 known amphibian species. Although up to 40% of the world's amphibians may be declining, the percentage of "Data Deficient" species (23.4%) is very high for amphibians compared to mammals (5.3%) and birds (0.8%). This category has inadequate information to make an assessment of its

TABLE 1. Abbreviated version (minimum set of information) required for non-marine taxa in the IUCN Red List of Threatened Species (IUCN 2001).

Scientific name including authority details
English common name/s and any other widely used common Red List Category and Criteria
Countries of occurrence (including country subdivisions for large nations)
A map showing the geographic distribution (extent of occurrence)
A rationale for the listing (including any numerical data, inferences or uncertainty that relate to the criteria and their thresholds)
Current population trends (increasing, decreasing, stable or unknown)
Habitat preferences (using a modified version of the Global Land Cover Characterization (GLCC) classification
Major threats (indicating past, current and future threats using a standard classification which is available from the SSC)
Conservation measures (indicating both current and proposed measures using a standard classification which is available from the SSC)
Information on any changes in the Red List status of the taxon, and why the status has changed
Data sources (cited in full; including unpublished sources and personal communications)
Name/s and contact details of the assessor/s

risk of extinction based on its distribution, abundance and population status (Hilton-Taylor 2000).

Status reviews are often the first step in a listing process in the U.S. (Henifin et al. 1981; USDI and NOAA 1996). These activities are funded or conducted by one of the federal agencies or others to determine the status of a species and include field surveys, museum research, and literature searches to compile complete information. Status reviews are required by the Endangered Species Act and are suppose to include all of the available information on a species. A status review should also use the knowledge and external consensus of experts on the species.

Most of the information needed is based on natural history or field ecology studies. I completed one of these status reports in the mid-1980s on the Black Legless Lizard (*Anniella pulchra nigra*)—a dark color morph living near Monterey Bay of coastal California. We conducted field surveys prior to completing the set of required questions (see Table 2). Most of our prior knowledge was based on a major field study about 40 yrs earlier (Miller 1944). Clearly, a solid report should have wide scope to document the range of variation in habits and habitat requirements across the geographic distribution of a species as well as several intensive studies at representative sites to determine key population features (e.g., demography, population estimates, and fecundity). Such assessments, however, are often inadequate because we lack even the basic information on most of our herpetofauna.

It is difficult to undertake effective conservation of species if we have spotty, outdated and minimal data on life history features. We have knowledge of natural history or ecology for only a few common or widespread species, such as the Slider Turtle (Gibbons 1990), Desert Tortoise in the Sonoran Desert (Van Devender 2002), and Gila Monster (Bogert and del Campo 1956; Beck 2005). There are efforts on some species groups, including: box turtles (Dodd 2001), North American tortoises (Bury and Germano 1994), garter snakes (Rossman et al. 1996), and U.S. amphibians (Lannoo 2005). Species that have much known about them are often those that are hunted (e.g., American Bullfrogs; see Bury and Whelan 1984) or listed as threatened or endangered.

For most other species, I think that today we know less proportionally—compared to the increase in overall knowledge in biology—about their distribution, habits, abundance and trends than we did in the past. In large part, this is due to prior research and studies in landscapes with few human perturbations (roads to pesticide use). What we knew about a species in a pristine area decades ago may have little relation to what the populations face today because our imprint has grown rapidly across the landscape.

Thus, studies of life history and natural history are essential for the survival of our biota. One cannot make intelligent management decisions without range-wide data on species. Now, we must focus studies on the ecology of populations and species where human perturbations occur (i.e., do not just study a species in a pristine habitat).

There is a glaring need to have recent information on species'

TABLE 2. Outline used for a listing of U.S. Federal threatened or endangered species. Categories based on Henifin et al. (1981) and the U.S. Endangered Species Act. Not shown are parts for information sources and authorship.

Species information

1. Classification and nomenclature
2. Present state status
3. Description
4. Geographical distribution.—Includes populations currently or recently known extant; those known or assumed extirpated, with explanation; historically known populations.
5. Environment and habitat.—Summary of the most important aspects of these criteria, particularly those factors thought crucial to the taxon's survival, distribution, and abundance.
6. Population biology.—General summary; demography with number and geographical spacing of known populations (estimated if necessary), with estimates of currently known number of individuals per population, if available. Describe census methods used.
7. Current ownership and management responsibility.
8. Evidence of threats to survival.
    a. Present or threatened destruction, modification, or curtailment of habitat or range.
    b. Over-utilization for commercial, sporting, scientific, or educational purposes.
    c. Disease or predation.
    d. Inadequacy of existing regulatory mechanisms.
    e. Other natural or manmade factors.

Assessment and Recommendations

9. Priority of listing or status change
10. Recommended critical habitat
11. Interested parties

distributions, ecology and population trends. Developing quantitative information on responses of biodiversity and ecosystem processes to perturbations is of priority (Noss 1999; Dayton 2003). Experimental tests of concepts are needed, yet they are far from comprehensive because, among other reasons, many species are yet unknown or difficult to measure (Schulte et al. 2006). There are several national programs now underway such as the Partners in Amphibian and Reptile Conservation (PARC) (http://www.parcplace.org) (Gibbons 2000) and the Amphibian Research Monitoring Initiative (Corn et al. 2005; Muths et al. 2005). Still, the task ahead is onerous, and we need more effective means to gather information and communicate the results of research and conservation efforts.

CONCLUSION AND RECOMMENDATIONS

Natural history and field ecology are essential building blocks for a comprehensive education about not just herpetofauna but for key biological questions and collaborative work (Fig. 1). Learning how to observe animals and their lives in the wild will improve one's ability to pose key ecological questions. Natural history and life history studies are mandatory elements for conservation and management purposes (Fig. 1), and merit major infusions of funding.

To be a "naturalist" one needs to develop critical thinking skills, test hypotheses, have intellectual curiosity and maintain competence in several disciplines or endeavors. Thus, being a naturalist may be a skill set embedded in more modern labels such as conservation biologist, evolutionary ecologist or restoration ecologist. These all are part of a larger process (Fig. 1). I support the guidelines and advice of other scientists who have commented on the topic:

- Given the rapid loss of species now occurring as the result of human actions, academic training in natural history should receive high priority (Stebbins and Cohen 1995).
- Natural history is far from dead, but today is a flourishing enterprise (Arnold 2003). Further, he stated that the future of the naturalist's tradition lies in concept development and, of utmost importance, that mutual respect and collaboration among disciplines best serve our own mental health as well as the future of natural history.
- Remove the impediments to natural history, including excessive technophilia, little funding, elitism on the part of some biologists and a shortage of journals that publish organismally focused studies (Greene 2005).

Studies of natural history, life history and field ecology provide the factual information to address critical environmental issues, particularly the gathering and interpretation of the best biological data for the listing of species as threatened or endangered as well as the factors leading to their declines. The importance of field data and thorough status reviews cannot be underestimated because once a species is listed, it often triggers a multi-million dollar recovery effort for the species. Moreover, the timeliness of information becomes apparent when we admit that all too often the most detailed field studies and data sets were ones conducted decades ago, and recent data are scant.

Thus, we have several needs: (1) accurate and timely information on populations; (2) more intensive studies of life history features as well as current distributional limits and population trends; and (3) merger of the best natural history and field ecological data with the latest advances in genetic analyses, landscape ecology and other fields of inquiry. Communication between varied disciplines and fields of study and management is important to advance science and to address our key environmental issues. It takes a scientific community and many concerned parties to save a species, let alone an ecosystem. We must connect these dots to see the big picture.

Toward these goals, we hope that the new journal *Herpetological Conservation and Biology* will provide a forum and home for research and discussion on conservation and management issues. We should recognize the importance of natural history and not shy away from its role in science. In particular, we require more published material (peer reviewed) to better conserve and manage our amphibians and reptiles.

It is time to rekindle the spirit of inquiry, passion and excitement of field research and study of natural history. Thus, I suggest that

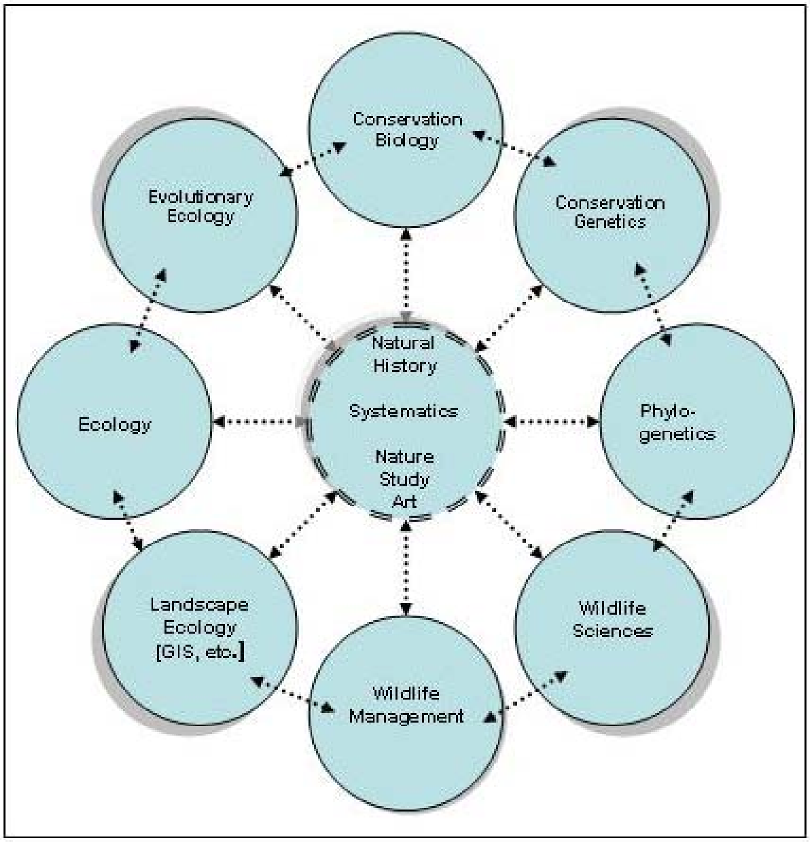

FIGURE 1. Representation of interrelationships of biological disciplines.

we do not lose sight of why most of us study animals and try to protect natural resources. This is best said by two of our distinguished colleagues:

> "*I regard inquiry as the greatest pursuit of man…. One of the richest sources of subject matter is to be found in undisturbed portions of the biosphere…*
>
> *As wild animals disappear, our own lives are endangered, for their well-being is intimately tied to our own. Their plight warns us of imminent ecological danger to man himself. It is the nature of the web of life that this should be so. We must not allow this priceless heritage to be degraded.*"
>
> Robert C. Stebbins (1971)

> "*It seems to me that the natural world is the greatest source of excitement; the greatest source of visual beauty; the greatest source of intellectual interest. It is the greatest source of so much in life that makes life worth living.*"
>
> Sir David Attenborough (2006)
> http://www.bbc.co.uk/nature/programmes/tv/lifeonair/faq.shtml

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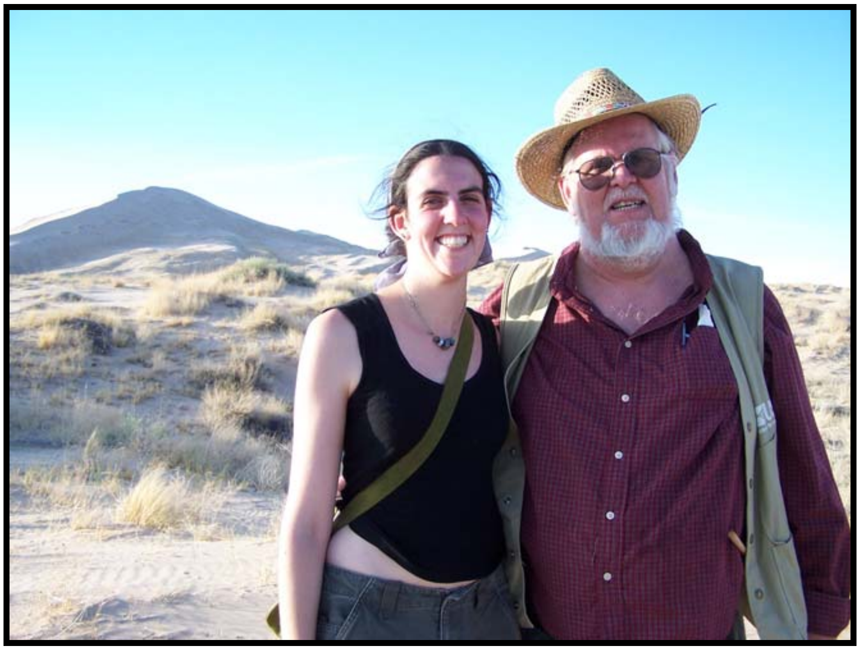

R. BRUCE BURY is a Research Zoologist with the USGS Forest and Rangeland Ecosystem Science Center, Corvallis, Oregon. He is pictured here with his daughter, Gwendolynn, at the Kelso Dunes, Mojave National Reserve, California. This was in early June 2006 just after the first organizational meeting of *HCB* in Henderson, Nevada. He was born in southern Oregon and grew up in northern California, where he attended Humboldt State University (A.B.), Calif. State University - Sacramento (M.Sc.) and the University of California at Berkeley (PhD). He has authored 150 publications, mostly on forest amphibians and desert reptiles in the western United States. (Photographed by Roger A. Luckenbach)

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PUBLICATION TRENDS OF NATURAL HISTORY AND FIELD STUDIES IN HERPETOLOGY

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***Abstract.*—Although natural history studies provide important information on the life histories of amphibians and reptiles, their publication has gradually declined over recent decades. We compared publication of natural history and total articles in *Herpetologica* and *Journal of Herpetology* over the lives of these two journals. We analyzed data using trends analysis and the individual trends with regression techniques to describe changes in publication frequency. In *Herpetologica*, the number of natural history articles increased from 1936 through the 1960s, but these manuscripts were often short notes and isolated observations. The number of total publications and of natural history publications remained stable through the late 1960s. Although the total number of articles published in *Herpetologica* has declined in more recent times, the relative number of life history publications has dropped much faster than the total production. Both the numbers of natural history articles and all articles increased since the founding of *Journal of Herpetology*, but natural history articles have dropped substantially since the mid-1990s. When combining publishing trends for both journals, there was an obvious decrease in the proportion of natural history articles. Explanations for these reductions are complex but may include less grant funding, editorial decisions, additional competition from other journals, and the rise of molecular biology and genetic studies. Many of the 'natural history' papers may have migrated to regional journals, foreign outlets, or one of many new specialized journals.**

Key Words.— conservation, *Herpetologica*, herpetology, *Journal of Herpetology*, natural history, publishing

Defining the biodiversity of our planet goes beyond describing structure and phylogeny. Biodiversity is also defined by how the environment molds life history characteristics (a.k.a., natural history) within and among species. Therefore, the basic biology of an organism provides critical information for developing models and testing questions of importance to evolution (Mayr 1963), environmental issues (Anderson 1985; Clemmons and Bucholz 1997; Schneider and Root 2002) and clinical topics (Mayer 2004). Natural history traits are the result of natural selection on the individual which drives the makeup of a population (Stebbins and Cohen 1995) and it forms the foundation upon which advanced biological research and conservation strategies are built (Greene 2005). Meaningful question-driven research requires in-depth data collection of natural history information. Further, we derive the information necessary to implement conservation strategies from the organism's basic biology or natural history (e.g., see Bury 2006).

Natural history data are key elements of biodiversity studies and must be statistically robust, of sufficient sample sizes, and temporally and geographically representative (Greene 1993). These considerations require a firm understanding of study design (e.g., danger of pseudoreplication; see Hurlbert 1984) and the biological levels of organization. Also, they should be focused on natural history and not embedded in other kinds of research.

The volume of natural history articles being published may be declining fast (Lunney 1998). Others suggest that natural history is thriving and dominating outlets outside the herpetological community (Arnold 2003) or being embedded in other studies. Here, we examine publishing in two herpetology journals to determine how natural history publishing has varied over their lives and discuss the implications of these patterns.

MATERIALS AND METHODS

Because the *Journal of Herpetology* and *Herpetologica* are the two major North American journals focused strictly on herpetology, we chose these as the focus of this study. We reviewed 62 volumes of *Herpetologica* published from 1936–2003 (Volume 4, 19, 38-39, 49, and 52–54 were not available for examination and were excluded from this study) and 37 volumes of the *Journal of Herpetology* published from 1972–2003. We assembled a list of research areas that we used for categorizing manuscripts (Table 1). Often this information was embedded in manuscripts focused on questions of phylogeny or ultimate function ('why' something happens [Tinbergen 1963]) making the data difficult to identify. Any confirmatory (tests a hypothesis) or exploratory (proposes a hypothesis) article (for a discussion of these two approaches see Jaeger and Halliday 1998) containing new, original life history information was tabulated as a natural history article. Any attempt to document natural history articles will have a degree of subjectivity involved, and this study is no different. Still, we made every effort to accurately portray and represent what is and what is not a natural history article and to take the most inclusionary and liberal approach possible to classify manuscripts. Articles that focused on phylogeny, systematics, genetics or molecular biology, ultimate function, or other areas without contributing new life history data were generally not classified as natural history articles.

We subjected tabulated data to linear trends analysis and linear regression using Minitab 14.0 (Minitab, Inc.). We analyzed the publication patterns of both journals combined and each journal

TABLE 1. An abbreviated list of areas for life history and ecology studies with amphibians and reptiles.

Reproduction and Development
- Hybridization
- Karyotypes
- Inheritance
- Induced spawning
- Fertilization
- Developmental period
- Hatching
- Intersexual variation
- Geographical variation
- Environmental affects
- Embryonic development
- Early life history
- Periodicity
- Courtship
- Parental care/mate guarding
- Spawning site
- Spawning period
- Gamete viability
- Fate of breeders
- Spermatic/ovulatory cycles
- Fecundity
- Fitness
- Post-breeding behavior
- Factors influencing growth
- Relation of sexes and kin selection
- Longevity (average/maximum)

Species Relationships
- Parasitism
- Commensalism
- Symbiosis
- Mimicry
- Predation
- Predator evasion
- Competition

Biogeography
- Original and current distribution
- Influencing factors
- Local distributions

Habitats and Associations
- Stress tolerance
- Thermal
- Salinity
- Daily, seasonal, etc., habitats use
- Community associations

Morphology/anatomy
- Coloration/patterns/morphs
- Sexual dimorphisms
- Life history stage characterization
- Organ weights
- Teratology
- Length & weight associations

Gastroenterology and feeding
- Bioenergetics of feeding
- Selectivity and diet composition
- Foraging economics
- Factors influencing food eaten
- Biomechanics of feeding
- Feeding behaviors
- Periodicity of feeding
- Daily food requirements
- Nutrition
- Food conversion rates
- Seasonal diet variation
- Temperature association
- Seasonal anatomical changes

Populations
- Mortality rates
- survivorship/recruitment
- Relative/absolute abundance
- Demographics
- Disease
- Conservation/management
- Seasonal, geographic
- Yearly patterns

separately to reveal the patterns (N papers/yr) of total, natural history, and non-natural history publishing which have occurred over the life of these journals.

RESULTS

Herpetologica.**—**Number of papers was erratic early in its history, but stabilized to about 10–20 articles per issue by the 1970's (Fig. 1). From 1936–1964 *Herpetologica* published a mean of 14.7 (SD = 8.2) articles and 7.6 (SD =5.6) natural history articles per issue. There was little difference (2.2%) between total and natural history publishing in the journal during this period. Natural history articles increased from 1936–1964 (Fig. 2; r^2 = 0.317, P < 0.001) despite an obvious shift from publications characterized as short "natural history note" type manuscripts, to larger research manuscripts with extensive datasets. Then the total volume of articles stabilized in *Herpetologica*, but the number of natural history articles declined in 1970-2003 (r^2 = -0.630, P = 0.001) 13.8% faster than total publishing (r^2 = -0.506, P = 0.001). Non-natural history publishing remained stable during this same period (r^2 =0.040, P = 0.327). The proportion of published articles that focused on natural history also declined (r^2 = -0.242, P = 0.011).

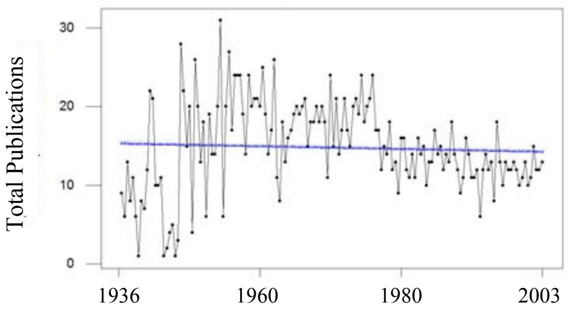

FIGURE 1. Total publishing in *Herpetologica* 1936–2003. Points are observed values and the line represents the trend.

Journal of Herpetology.**—**The total number of articles published increased since its first issue (Fig. 3). Publication of natural history articles increased dramatically (Fig. 4; r^2 = 0.597, P = 0.001) since its founding, but rose 10.5% slower than total publishing and dropped since 1993. Currently, *Journal of Herpetology* publishes a mean of 14 (SD = 3.5) natural history articles and 24 (SD = 5.0) total articles per issue. Publication of non-natural history articles remained stable throughout this same period (r^2 = 0.099, P = 0.117).

Combined publishing.**—**Total combined publishing increased since 1973 (Fig. 5a; r^2 = 0.161, P = 0.042). The number of natural history articles did not increase (Fig. 5b; r^2 = 0.010, P = 0.634), although publication of non-natural history articles increased (r^2 = 0.141, P = 0.059).

DISCUSSION

Our results suggest that the number of papers on natural history and species ecology data in herpetology journals is stable or declining relative to other types of articles. This is occurring when we need increases of such work for conservation and biodiversity management professionals (see Bury 2006). Of particular concern is the nearly 20% overall reduction in articles containing natural history.

Possible Reasons for the Decline.**—**There are many reasons that could reduce production or acceptance of natural history studies in herpetology journals. Editorial decisions played a critical role for *Herpetologica* (Robert Jaeger, pers. comm.) as this journal gradually altered its focus to "question driven" research while shying away from all but exceptional descriptive studies.

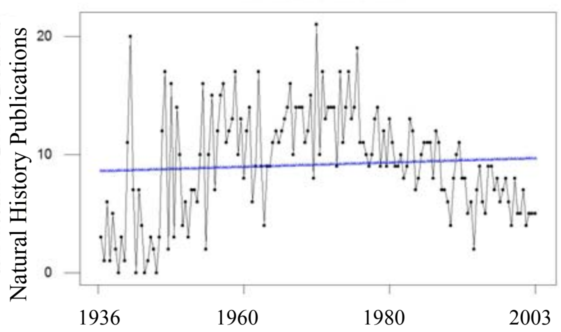

FIGURE 2. Publication of natural history articles and articles containing natural history information in *Herpetologica* 1936–2003. Points are observed values and the line represents the trend.

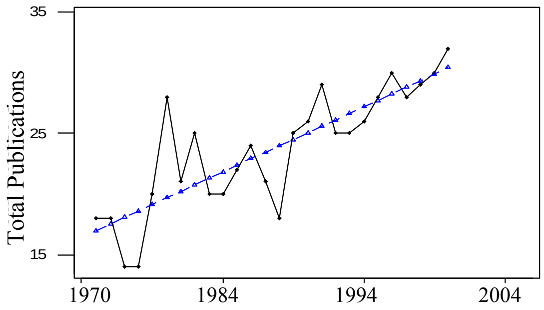

FIGURE 3. Total publications in the *Journal of Herpetology* 1973–2004. Points are observed values and the line represents the trend.

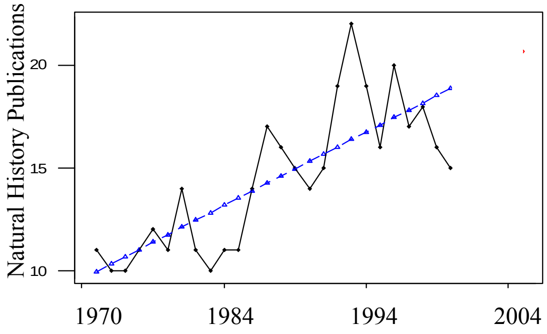

FIGURE 4. Publication of natural history articles and articles containing natural history information in *Journal of Herpetology* 1973–2003. Points are observed values and the line represents the trend.

Although *Herpetologica* regularly rejected natural history manuscripts during this period, the *Journal of Herpetology* continued to publish these kinds of submissions. The number of herpetologists has proliferated dramatically since these decisions were made (Altig 1989) and competition for page space within the primary herpetology outlets increased. This trend may have squeezed out natural history and field ecology studies. These studies are now often found in other outlets with more regional foci (e.g., *Southwestern Naturalist*).

The need for expansion of natural history research follows that which transpired in the systematics community after a steep decline in systematics research. The United States National Science Foundation (NSF) established a grant program dedicated to increasing systematics training opportunities. This action led to increased publication in this important field. By 1989, the growth of modern molecular and mathematical techniques was accompanied by the loss of funding in systematists (NSF 2005). One of us (Malcolm McCallum) recalls hearing faculty say, “Systematics is dead” when he was an undergraduate during the 1980s. Recently, some university professors are declaring the same of natural history (see Bury 2006). This seems to run counter to declarations that it is alive and thriving (Arnold 2003). In response to a recognized accelerating loss of biological diversity, the U.S. National Science Board inspired the U.S. National Science Foundation to develop programs to circumvent declining numbers of systematists (NSF 2005). The goal was to “increase the number of systematists so that we could accurately document the biodiversity present on the planet.” This was needed because of the “Retirement of taxonomic specialists, shifts in academic recruitment and staffing, and reductions in graduate training opportunities.” These situations were declared to “impede biodiversity research and conservation, particularly of poorly known groups of organisms” (NSF 2005). Today, we have a much more secure and technologically advanced systematics infrastructure; whereas, natural history continues to disappear from the research scene.

The introduction of genetics and molecular biology into the

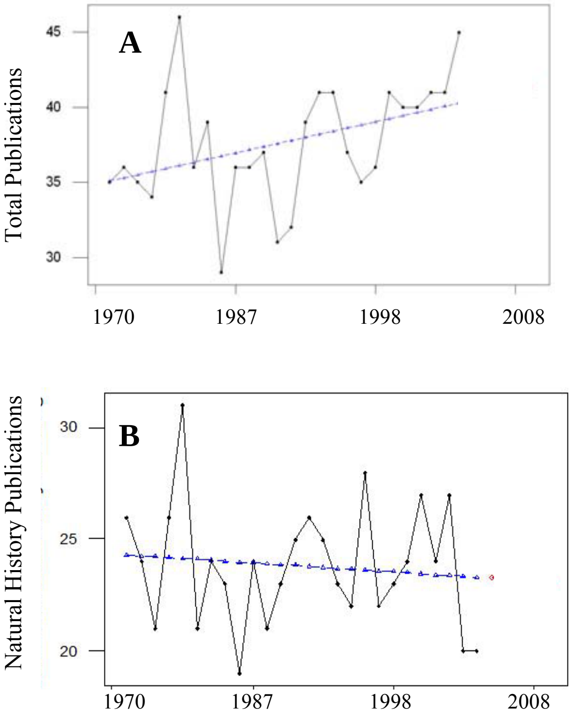

FIGURE 5. Combined publication patterns between *Journal of Herpetology* and *Herpetologica*. Points are observed values and the line represents the trend. A) Total number of manuscripts published by both journals combined has increased since 1973. B) Publication of natural history publications and articles containing natural history information has decreased since 1973.

research arena undoubtedly created significant competition for financial, human, and technical resources. Natural history research surely continues to suffer as these other growing fields expand (but see Arnold 2003). An examination of the herpetological literature will reveal considerable inroads by molecular biology into systematics, conservation and evolutionary ecology. Molecular approaches now dominate modern systematics, but technologically advanced approaches (e.g., radio isotope diet studies, genetic fingerprinting) are expensive to justify for natural history work unless the focal species has conservation status. Geographic information systems and their associated extensions are probably the only new technology that became widely adopted by natural historians. Although most natural history investigations do not require technologically advanced and novel approaches, incorporation of these techniques can improve the odds that a natural history article will be published. In fact, most natural history publications in highly rated journals involve some form of advanced technology or species of conservation concern (our anecdotal observation).

Consolidation and closure of many university museums (a key resource used in status reviews, see Bury 2006) probably also contributed to the reduction in natural history work as well. Natural history studies frequently use museum deposited specimens for investigation. The researcher lacking travel funds and access to museum collections cannot obtain enough specimens to adequately describe life history characteristics leading to abandonment of this line of work in favor of more fundable research areas. This situation creates negative feedback because for natural history studies to be useful they must be permanently archived (Greene 1993). As more researchers cease natural history work and field biologists retire, there remain fewer opportunities to properly train candidates in this important area of biodiversity studies. Consequently, the climate for natural historians studying the Earth's biodiversity mirrors that which was present in systematics when NSF implemented programs to reduce the shortfall of experts.

The current academic climate does not foster natural history research, especially long-term studies (Fitch 2006). Many universities require specific grant numbers and dollar values for superior faculty evaluations. The moderate number of government biologists studying natural history is also declining as administrative tasks continue to grow and increasingly dominate their time and responsibilities. No grant-funded programs currently support training natural historians and none are dedicated strictly to natural history research (NSF, pers. comm.). Natural history research on common species must be attached to larger questions or embedded within other areas of research (NSF, pers. comm.). Essentially it is an after thought to "fundable research." By placing low priority on life history investigations our society has unintentionally placed conservation needs for common species on the backburner. If a species declines enough, reactive measures will make funding available. However, many logistical problems exist and proactive approaches to funding natural history research are needed to avoid or prepare for imminent declines.

What Does This Mean to Science and Conservation Efforts in Herpetology?— Natural history studies are generally focused on the organism and its response to its environment (Greene 1986, 2005). The immediate aim is to "describe fully and accurately everything that is seen" (Green 1993) and to develop hypotheses for future study (Jaeger and Halliday 1998). This requires substantial dedication and skill, despite the general belief that it is chiefly anecdotal, requiring no forethought, perspective, or special training (Greene 1986). In fact, natural history study requires a voluminous knowledge of biodiversity. Because of the skill required (Table 1), there are several detailed outlines of important areas for natural history studies (Anonymous 1933; Fitch 1949; Cagle 1953, 1956). Despite this, the ability of the scientific community to conduct solid natural history and field ecology studies continues to decline (Greene 1993; Lunney 1998).

Operationally, the natural historian is more of a hypothesis generator while most ecologists are hypothesis testers (Jaeger and Halliday 1998). Few biologists play both roles, but this is feasible. With a demonstrated reduction in the publication of natural history articles, we should be concerned with how this may impair our conservation efforts in the face of looming biodiversity declines.

Biodiversity conservation requires description of critical natural history parameters (Table 1; Schultz et al. 1999). These parameters are poorly known for most herpetofauna (Stuart et al. 2004; IUCN [International Union for the Conservation of Nature], Conservation International, and NatureServe. 2006. Global Amphibian Assessment. http://www.globalamphibians.org. Downloaded on 9 August 2006.). Early life history, which is an active area of research in ichthyology, is infrequently studied for most species of amphibians and reptiles. Until life history information is acquired, we must hypothesize or speculate on this information needed for modeling population responses to environmental problems. This is inadequate.

Conservation of amphibians and reptiles necessitates life history inquiries while the species are common and their populations are ecologically functioning. Environmental stressors frequently influence life history characteristics early in the stress response (Newman and Unger 2002). Consequently, waiting until a species is on the brink of extinction is too late to accurately estimate life history parameters consistent with a "healthy" environment. We sometimes base our conservation decisions on extrapolations from somewhat well known species or surrogates (Newman and Unger 2002). Most of our decisions for herpetofauna are based on organisms that are distantly related both systematically and ecologically. The natural history of an organism defines its place in the ecosystem and reveals its conservation needs (Greene 2005). Without attention placed in this vital area of biodiversity study, any attempt to significantly improve the conservation status of amphibians and reptiles will be compromised.

We recommend that granting agencies (e.g., NSF) follow on the rationale used to implement the NSF program for systematists and initiate funding and training programs that targets the heart of the amphibian decline question: the lack of life history information. We further encourage those training graduate students to ensure that these young investigators develop the skills necessary for both inquiry and descriptive studies. Finally, we challenge scientists, especially those who are no longer seeking tenure or promotion, to dedicate at least part of their efforts to natural history study and to encourage young researchers to pursue research in this important area of herpetology. By doing these things we can ensure that our study of biodiversity reveals information critical to the conservation needs of herpetofauna. Without these efforts, the opportunity to observe these intriguing animals and their unique position in the biosphere will be lost.

We hope that this new international journal published in concert with Partners in Amphibian and Reptile Conservation and the World Congress of Herpetology will provide an important outlet for studies ranging from descriptive natural history to theoretical approaches in conservation and ecology. A publication of this kind is important to facilitate dissemination and exchange of information within the scientific and conservation communities. We desire for this journal to stimulate research activity in these areas. Although the launch of *Herpetological Conservation and Biology* appears to be counter to the declining publication trend of natural history and many field studies, there remains a growing critical need for information on the basic biology, conservation, ecology and management of amphibians and reptiles.

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A PERSONAL GLIMPSE INTO NATURAL HISTORY AND A REVISIT OF A CLASSIC PAPER BY FRED R. CAGLE

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***Abstract*.—Herein, I provide perspectives on natural history studies and discuss the importance of a contribution by Fred Cagle to herpetology. Having studied the natural history of many amphibians and reptiles for 35 years, I recognize the importance of developing a research strategy prior to beginning work. Cagle's manuscript is a detailed outline of what directions an investigator can take when developing a research strategy in natural history. His thorough approach provides any interested scientist a bounty of questions worthy of scientific study.**

Key Words.—natural history; herpetology; reptile; life history

My editorial colleagues and I feel that it is appropriate in this inaugural issue of *Herpetological Conservation and Biology* that we revitalize awareness about natural history studies. Thus, our first Special Features Article is a reintroduction of the seminal paper on the science of natural history by Fred R. Cagle (1953). We provide a PDF based on the permission of The Editor, Tulane Studies in Zoology and Biology. (To obtain an original copy, contact: http://www.museum.tulane.edu/pubs/tszb.html.) Here, I draw upon several of my own research experiences and recollections as a way of recasting the essence of natural history questions as summarized by Cagle (1953).

First, I note that Cagle (1953) introduced his article by encouraging systematists to not ignore the growing field of ecology and vice versa. Later, Greene and Losos (1988) also emphasized the combined role of systematists, as well as natural historians in preserving biodiversity and changing the public image of field biology. Only through the bridging of various modern biological disciplines, from molecular ecology and genetics to biogeography and field ecology, can the urgent needs of global conservation be adequately addressed.

Cagle (1953) outlined many avenues to investigate reptilian life histories. He provided a lengthy hierarchical list of primary, secondary, tertiary, quaternary, and even pentacular-level questions. The first two primary questions address identifying the species at hand, and the next six can be roughly divided into the categories of reproduction and population dynamics. Primary questions 9 and 10 examine seasonal and daily activity patterns, whereas 11 and 12 address food habits and group behavior, respectively. This litany of questions occupies the first 17 pages of the article; the Literature Cited includes 114 citations (the last 6 pages). Cagle used many citations involving research techniques that were borrowed from other zoological disciplines and were not necessarily applicable to reptiles—a remarkable vision on his part to learn from other sources. One of his most noteworthy statements still resonates today: "*A serious report on a life history should be the result of a planned, long term, research project.*"

As a field researcher of amphibians and reptiles for 35 years, I have studied most aspects of herpetological natural history (e.g., geographic variation, distribution, life history, reproductive cycling, movement patterns, food habits, etc.). Furthermore, I have investigated amphibians and reptiles in the laboratory by incorporating histological and electron microscopic analyses. For example, some life history questions related to the timing of reproductive events (e.g., phenophases) can actually be addressed more effectively at the tissue and organ level (see comments below) than through field studies. A lesson here might be that a useful strategy prior to beginning work as a biologist is to become multidisciplinary in your technical and research skills (by combining lab as well as field techniques) and consider answering "Cagle's questions" from several investigational directions and viewpoints.

My devotion to the study of amphibians and reptiles began when I was a zoology undergraduate student enrolled in the Natural History of the Vertebrates taught by Dr. Douglas A James during the late 1960s at the University of Arkansas at Fayetteville. I can still vividly recall my first class field trip. We went to a local farm pond that was a breeding site for Spotted Salamanders (*Amybstoma maculatum*). The excitement generated by the students while seining for and finding these salamanders in the cool darkness of a January night was pivotal in leading me into a career in science with a specialty in herpetology. It was "natural history" that caught my interest then and holds it even now.

Upon entering graduate school in 1971 and following the advice of my advisor, Dr. James M. Walker, I selected field ecology of lizards as a starting point for my fledgling herpetological career. I grew up chasing Eastern Collared Lizards (*Crotaphytus collaris*) in cedar glade habitats in northern Arkansas, and a chance to conduct thesis work on this colorful saurian was my good fortune. My initial literature search prior to starting my field investigation yielded two 'must have' articles: Fitch (1956) and Cagle (1953). The first introduced me to the natural history and published literature on this spectacular lizard, and the second provided a plethora of literature and techniques and also detailed those important questions that could be pursued within the context of any reptilian natural history study. It was one of Cagle's tertiary questions (p. 40) that most grabbed my attention: *"How many groups or young (eggs) are produced each year?"*

This question forced my thesis work into the lab for a seasonal histological analysis of ovaries to identify atretic follicles, corpora lutea, and corpora albicantia (see Trauth 1978) and, eventually, lead me into an academic career as a comparative reproductive anatomist (histo-herpetologist). However, I still like to think of myself as a field herpetologist.

The first two of Cagle's primary questions remain as critical reminders to all scientists studying wide-ranging species: *"What are* *the morphologic characteristics of the population to be studied?"* (p. 32) and "*What is the geographic range?*" (p. 34). These became apparent to me when I was examining the external morphology of three known subspecies of racers (genus *Coluber*) that were known to occur throughout Arkansas during the mid-1990s (Conant and Collins 1991). I just happened to observe that several of my photographic color slides of adult snakes from eastern Arkansas revealed specimens that exhibited rather well-defined, dark, postocular stripes. This morphological feature led to the discovery of a fourth geographic race of this species, the Blackmask Racer (*C. constrictor latrunculus*), which presumably had extended its range northward and westward from Louisiana and Mississippi, respectively, and now apparently occupies much of the Delta of eastern Arkansas (Trauth 1997; Trauth et al. 2004).

Another instance in which these two questions became relevant was in an analysis of the geographic variation in Ringneck Snakes (*Diadophis punctatus*) in Arkansas. When Upton et al. (1995) named a new coccidian parasite from a specimen of the Prairie Ringneck Snake, *D. p. arnyi*, from western Arkansas, I also recorded the presence of the Mississippi Ringneck Snake, *D. p. stictogenys*, in close geographic proximity to the infected snake. This observation prompted me to conduct a state-wide morphological analysis of Ringneck Snakes that resulted in the discovery that the range of *D. a. stictogenys* extends well into the Interior Highlands of Arkansas (Trauth 1996) and is not restricted to the Gulf Coastal Plain and Delta as was previously understood (Conant and Collins 1991).

I utilized one of Cagle's tertiary questions, *"How do the eggs vary in size, volume and weight in each clutch?"* (p. 41), during a study of lizard nesting sites and egg clutch characteristics (Trauth 1983). By unearthing numerous egg clutches of the Six-lined Racerunner (*Aspidoscelis sexlineata*) from its nesting habitats and by analyzing egg volumes, I determined a variety of life history traits for this species, such as egg volume at the time of oviposition, the length of the nesting season, the change in egg- clutch mass during the incubation period, and the number of clutches deposited per nesting season. This line of research also led me to examine eggshell morphology in this species using electron microscopy (EM; Trauth and Fagerberg 1984), and that experience served as a springboard for many later EM studies.

These selected examples illustrate why the questions posed by Cagle (1953) and by his subsequent outline on amphibians (Cagle 1956) are timeless and, thus, greatly beneficial to all young herpetologists as starting points for career research. Cagle's life-history questions were acquired from many previous investigators and, not surprisingly, included valuable suggestions from a timely paper by Fitch (1949).

While preparing these introductory remarks about the significance of natural history in contemporary herpetological studies, I have also chosen to revisit two notable literature sources. First, there can be no better review articulating the importance of retaining research in natural history than Greene and Losos (1988). Their message to the scientific community resounds clearly and profoundly today: get personally involved in educating society about what field biologists and systematists do or witness the demise of public support for field biology. If by some chance you are unfamiliar with Mitchell (1979), then you are probably not fully aware of how to become actively engaged in studying herpetological natural history on a temporal basis. He summarized an important concept that literally drives herpetologists into the field to perform observational studies in natural history. Our understanding of how the elements of the biotic and physical worlds interact on an annual cycle is tied into the concept of phenology, which is defined as the seasonal sequence or timing of life cycle events. Practitioners involved in herpetological conservation and biology continually add to an ever-increasing phenological database and utilize this knowledge to detect and decipher variations in life history patterns. Natural history studies normally focus on where animals occur and what they do (Greene 1994). To declare oneself a natural historian in herpetology in today's academic environment (specifically, the post-graduate job market), however, can be a risky stand, given the perception by many biologists that natural history research is either outdated or unessential. Critics argue that observational studies lack the scientific rigor seen in experimental, hypothesis-testing research. The most often asked question is why life history phenomena of natural populations should be studied by today's scientists anyway.

There are in fact a multitude of obstacles blocking this type of research. At present, extramural funding sources for field biologists are overwhelmingly in the areas of applied and/or technical field research, and what research is fundable often becomes the primary dictator of the direction or line a biologist's academic research pursuits follow. Granting agencies, potential employers, and even academic colleagues may argue that funding opportunities in natural history are nil, and by following this avenue of research, one will assuredly enter, research-wise, a 'black hole' or a 'dead end street'. Moreover, faculty researchers may sometimes be obligated to seek funding opportunities in step with their institution's stated mission and goals, which must meet the financial notion of cost-benefit research or fall within a most-appropriate grantsmanship activity. In accordance, graduate students entering herpetology generally pursue research options and degrees under scientists who offer the most competitive research stipends. Ultimately, the major focus of contemporary, cutting-edge research in herpetology has shifted away from the biology of organisms to understanding these entities as only mere models useful for conceptual study. This new reality is clearly evidenced in the primary literature of recent decades, which is now directed largely toward molecular genetic studies.

The editors of *HCB* are keenly aware of the ongoing conflict and increasing distance between molecular and natural history biologists. There are certainly many present-day ecological issues that may draw our immediate attention away from observational field investigations in herpetology. And yet, it is not surprising that many of the same fundamental questions, as outlined by Cagle many years ago, are totally relevant today. **Cagle remains an important landmark paper for reptilian study, which every herpetology student should read.** These questions require an understanding of basic biological phenomena, and as conditions change, their answers must be continually reexamined. By providing this special feature, the editorial staff hopes to enlighten novices and, at the same time, rekindle the imaginative spirit of veteran experienced herpetologists about the continued importance and application of natural history techniques in all of our herpetological pursuits.

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AN OUTLINE FOR THE STUDY OF A REPTILE LIFE HISTORY

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AN OUTLINE FOR THE STUDY OF A REPTILE LIFE HISTORY

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The renewed interest of biologists in natural populations, the development of the new systematics, population genetics, biodemography, and biosociology, i.e. of bionomics, or ecology in the broadest sense, has brought demands for detailed information on life histories of animals. The herpetologist is thus obligated to reexamine many of the standards and customary procedures in natural history. Renewed emphasis is also being placed on the organization of the knowledge comprised in natural history. Investigations in autecology (the ecology of the individual or of the individual species) are aimed toward the development of significant generalizations and principles. The modern systematist should not and must not divorce his thinking from ecology; the ecologist must not ignore systematics. While condemning the ecologist for ignoring systematics, the systematist has often been guilty of ignoring ecology. There is an urgent need for men thoroughly trained in the techniques of both ecology and systematics, men who can accelerate the trend toward a blending of these fields.

The investigator interested in reptilian populations finds but few studies of the bionomics of reptiles that meet critical standards. He finds an assortment of fragmentary facts that are difficult if not impossible to integrate, and often immediately require the test of repetition. It may be pointed out that repetition of field observations in a critical spirit may be fully the equivalent of experimental test. There seems to be a need for a statement of minimum requirements of information basic to the formulation of suggestions for a systematic approach to research on natural populations.

Perhaps the best test of significance of an observation in "natural history" is one similar to the test for the adequate description of a species or subspecies. Does the observation reflect an attribute of a given population? Is it reported in such a fashion that it may be integrated with other observations to state such an attribute? Or, has the research merely reported an aberrant or extreme behavior pattern, an anomalous situation, or such fragmentary data that it fails to express any particular fact as an attribute of a population?

What information is required in a definitive life history investigation? Ideally? What, practically, can the investigator hope to contribute? In what areas of biology may his data be applicable? What are the prevalent fallacies in life history analyses? Some attempt is made here to indicate limits and to designate specifically the obligation of the student interested in natural populations of reptiles. Many of the techniques developed by the ichthyologist, mammalogist and ornithologist may well be utilized by the herpetologist. There is an urgent need for the development of new techniques of research and for new applications of old ones. The herpetologist does not have the equivalent of the procedure of the ichthyologist for determining the age and growth of an individual by the examination of the growth lines of scales; nor does he have the trapping procedure for systematic sampling as used by the mammalogist, or the activity recording techniques developed by the ornithologist. Equivalents of these techniques are among our greatest needs. All of the needs for herpetological investigation cannot be enumerated in this paper, nor can all of the techniques developed in other fields be mentioned, but the bibliography is intended to provide suggestions and a key to the vast literature.

The herpetologist concerned with the study of a single form cannot hope to explore intensively all of the questions presented in the following discussion, but his awareness of the problems and of the need for information will permit him to make observations that otherwise might not be recorded. A serious report on a life history should be the result of a planned, long term research project. Such a report will integrate all of the minor elements of the topic to be gleaned from the literature with the more directed accumulation of planned observations of the author. The investigator, through proper planning, may maintain several such research programs. The outline that follows is purposely elaborated; and it includes much detail that may appear unnecessary to my colleagues; but it is directed to the students of the future who may be approaching similar problems from both the ecological and the systematic side. An early and comparable effort to systematize studies in life histories that has had a long usefulness is the summary of Walter P. Taylor (1919). Fitch (1949) presents many valuable suggestions for the student interested in natural history.

This paper is the outgrowth of an outline for the study of a reptile life history prepared originally under the direction of Dr. Norman E. Hartweg, University of Michigan. Its development has been encouraged by the critical and generous comments of Mr. Karl P. Schmidt, Chicago Natural History Museum. I am indebted to Mr. Roger Conant, Philadelphia Zoological Garden and Mr. Arthur Loveridge, Harvard University for their suggestions. The group of graduate students in herpetology at Tulane University has been a constant source of stimulating challenge in the preparation of this report. Mr. A. H. Chaney, Mr. Robert Gordon, Mr. Paul Anderson and Mr. Richard Johnson have been of particular aid.

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I. *What are the morphologic characteristics of the population to be studied? Is action taken to insure that the data reported are* *obtained only from individuals of the genus, species or subspecies intended to be studied?*

A. What is the taxonomic status of the population? What are the diagnostic features? How are these related to the formal description of the species or subspecies? Are these sharply or only obscurely characterized?

These data are of extreme significance. Excellent information must often be discarded by subsequent workers because the author has failed to indicate clearly the taxonomic characteristics of the population studied. Description must thus be such that any investigator can recognize the population regardless of changes in nomenclature.

B. What other names have been attached to this population?

C. What samples of the population were collected and preserved and where are they deposited? Museum numbers?

A representative series supporting the description given must be collected and deposited in a suitable museum collection. Failure to do this is almost characteristic of ecological investigations, yet the conclusion submitted are often not acceptable because of questionable identification of the material on which they are based.

D. What variation is observed in the individuals composing the population? Of what is this variation a reflection? Precise analysis and explanation of individual variation is an obligation. Dice (1952) points out that few museums have adequate storage or curatorial facilities to retain the large number of specimens necessary for the analysis of variation in local populations. The investigator must often utilize materials that cannot be available to future workers; his responsibility is thus multiplied. Through such studies associated with field investigations we may hope to accumulate the data basic to systematic studies at the intraspecies level.

1. What changes in color intensity, in pattern, or morphology occur from birth to old age? Are there any correlated sex differences? How are these changes related to taxonomic investigations? The limited information available on ontogenetic changes in "characters" has resulted in much confusion in taxonomy. The trend in herpetological research toward thorough analysis of such changes promises the development of a basis for substantial clarification of the status of many forms (Oliver, 1951).

2. Is the variation correlated with differences in the external environment?

With a gradient in the external environment? Is the

the variation due to differences in genotypes or does it reflect the responses of a specific genotype to different environments?

Investigations often query the status of the variation described but do not perform the simplest of experiments aimed at evaluating the genotypic flexibility of the organism studied. Some investigations suggest that some of the characters considered to be of taxonomic importance are merely phenotypic modifications (Fox, 1948). It is essential to the systematist that he determine whether variations are the result of heredity or environment or both.

3. What are the ontogenetic changes in mass as expressed by measurements or weight? What is the maximum size attained? Sex differences?

Although absolute size is not an acceptable taxonomic character for poikilothermic vertebrates, genetic differences in potential natural longevity or growth potentials may be reflected in differences in maximum sizes between populations (Lagler and Applegate, 1943).

What procedures were used in mensuration? Weighing?

Care must be used to insure adequate mensuration practices and to insure that the investigator clearly reports his procedures (Simpson and Roe, 1939; Cazier and Bacon, 1949). Much confusion has been caused by misunderstandings resulting from failure to specify the methods followed. The significance of the limits of error in such data should be borne in mind. When measurements are accurate only to millimeters, proportions calculated to three decimal places give a false aspect of accuracy of the data.

4. What are the principle differential growth changes in each sex? How are these changes related to the major phases of the life history?

Failure of the systematist to recognize the presence of differential growth has led to the erroneous use of proportions. If detailed quantitative studies cannot be made, the investigator should, as a minimum, designate the gross changes in proportion. This is a particularly acute problem in poikilothermic vertebrates (Hersch, 1941).

II. *What is the geographic range?*

The range should be expressed first in terms of museum specimens or records of authorities. All questionable records should be deleted. The range definition should indicate the distribution of existing populations (Grobman, 1950). These data may then, in connection with other information, form the basis for the statement of a supposed "true range".

A. What are the factors limiting the range?

These must be considered in terms of the ecological data assembled during the progress of the investigation with particular reference to the total knowledge of the ecological valence of the animal and possible barriers to dispersal (Darlington, 1948; Cowles and Bogert, 1944; Dice, 1952). It is especially important to note that the limiting factors may be entirely different on the different borders of the range of a species (Schmidt, 1950).

B. What physiographic and climatic factors are characteristic of the range?

1. What are the annual temperature and rainfall cycles?
2. What are the mean annual, minimum and maximum temperatures in the warmest and coldest parts of the range?

   Whenever feasible, temperature and rainfall data collected by the investigator in the areas of intensive study should be utilized. Of necessity, the investigator must often use meterological and climatological temperatures, but their interpretation should be based on the data of the researcher (Baum, 1950).
3. Does temperature summation (heat summation) affect the distribution of the species investigated?

C. What is the principal habitat? Marginal habitat?

1. Are microclimates of significance? throughout the range? at the periphery of the range? (Geiger, 1950; Diem, 1951).
2. What vegetational types characterize the habitat?
3. Do size or age groups tend to occupy different habitats?
4. Does the animal have an innate habitat recognition mechanism? (Svärdson, 1949; Tinbergen, 1948).

III. *What is the age and sex composition of a local population?*

A. What annual changes occur in the composition of a local population?

1. What is the sex ratio in mature individuals during the breeding season? How does this change during a single year?

   Sex ratios are often reported without reference to maturity or to the breeding season although radical changes do occur in some reptile populations. Estimates of the relation of sex ratios to natality should be based only on the relative frequency of mature individuals (Forbes, 1940; Cagle, 1948).

Sex identification is frequently reported without reference to the criteria used. What are these criteria? Secondary sex characters? Gonad condition? If dissection, on what basis was sex determined?

2. What is the sex ratio in juveniles? At birth? In progressive age groups?
3. What annual changes occur in the ratio of juveniles to adults? What is the potential contribution from "young of the year" to the adult segment of the population?
4. Can an ecological life table be constructed?

   The difficulty of determining mortality rates in most reptiles forbids the successful completion of such tables yet an attempt to collect data basic to the estimation of survivorship curves should be made (Deevey, 1947).
5. What are the major predators? Is predation pressure a significant factor in annual and long term cyclic changes? What is the relation of loss from predation to population density? (Errington, 1946).

B. What long-term cyclic changes occur in the composition of the local population? What is the cause of such cycles? Is exhaustion of the adreno-pituitary system a factor as has been demonstrated for some mammal populations? (Christian, 1950; Elton, 1942).

C. Do local populations differ in composition? If so, what is the basis of such differences?

Adequate local sampling provides a basis for obtaining answers to such questions. It has been demonstrated that substantial differences may be present in the compositions of local populations. Comparison of population samples must be tempered with an awareness of the difficulties of obtaining such samples. Series of specimens preserved in museum collections are rarely unbiased samples of natural populations. The student should note particularly those few long-term studies in local areas (De Haas, 1941).

D. Does the individual animal or the mated pair occupy a home range (or activity range as defined by Carpenter, 1952). Territory?

1. What is the size of the home range and of the territory?
   a. What features of the habitat may modify the size?

b. What is the relation of the size of the territory or home range to density?

c. Does the individual have homing ability? If so, what are the mechanisms involved in orientation?

The recovery of marked individuals in short-term and long-term studies will provide information on these questions. A wide variety of methods have been used for the marking of reptiles: metal bands or plates (Wickham, 1922); scale clipping (Blanchard and Finster, 1933; Conant, 1948; Fitch, 1949); plate notching (Cagle, 1939); tattooing (Woodbury, 1948); branding (Woodbury and Hardy, 1948); painting (Cagle, 1946). Trapping and other special collecting procedures are described by Dargan and Stickel (1949), Lagler (1943a). The calculation of size of home range from trapping results is discussed by Hayne (1949) and Stickel (1950). Stickel and Cope (1947) summarize information on home ranges. Schaefer (1941), Bailey (1952) and Leslie (1952) discuss the estimation of size of animal populations by marking experiments.

The multiplicity of problems involved in animal orientation are ably discussed by Fraenkel and Gunn (1940).

2. Is the territory selected by the male, female or both? Do both sexes participate in its defense?

a. What are the characteristic behavior patterns used in defense of territory?

Lowe and Norris (1950) summarize the reports of aggressive behavior in snakes.

b. What is the chief stimulus to maintenance of territory?

c. Is the territory maintained throughout the year or or only during short periods?

Nice (1941) presents a classification of the types of territoriality.

IV. *What is the density of the population?*

There should be more than a vague estimate of density expressed as rare, common or abundant. The objective should be to gain a measure of the number of individuals in a given area expressed in terms clearly defined by the investigator. The use of the concepts of abundance, and relative apparent abundance as suggested by Marr (1951) is recommended. The method selected for this determination of abundance must rest on the knowledge of the ecological requirements of the individual. Kendeigh (1944) provides a suggestive review of the procedures for measurement of bird population. Andrushko (1936) suggests techniques suitable for some species. A summary of methods is presented by Thomas Park (1950). Information of particular value in estimating populations from recovery of marked specimens is given by Ricker (1948), Jackson (1939) and Bailey (1952). This procedure has been applied to reptiles by several authors (Cagle, 1950; Fitch, 1949; Stickel, 1950).

A. What is the relation of density to the questions posed in sections I, D and III A to D (Blair, 1951)?

B. What is the relation of density of the form studied to that of other reptiles inhabiting the area? (Fitch, 1949; Cagle, 1950; Cagle and Chaney, 1950).

V. *What is the potential reproductive capacity? What is the relation to realized reproductive performance? What are the best measures of natality?*

A. At what age and/or size does the animal become sexually mature?

1. When are the secondary sex characters developed? What is the relation of time of their appearance to the potentiality of sexual functioning? (Regamey, 1935)
2. What cyclic changes occur in secondary sex characteristics?
3. What is the relation of age of attainment of maturity to the annual reproductive cycle?

Investigators often fail to indicate what they mean by sexual maturity. Care must be exercised that the criteria for maturity are defined. In reptiles these may concern the presence of oviducal eggs in females, of corpora albicantia, of ovarian follicles of a specified size or ovaries of a specified weight or volume (Altland, 1951). In males a specific stage of spermatogenesis, a specified testicle weight or volume in relation to an indication of total body mass or the presence of motile sperm may be useful (Cieslak, 1945; Cagle, 1944; Risley, 1938; Fox, 1952). No adequate techniques are available for determining the age of an individual reptile. The procedures used by Bryuzgin (1939) should be further explored. Bryuzgin concluded that rings discernible in cleared skull bones of snakes could be used to determine age.

B. What is the total period of reproductive activity in the life of an animal?

1. Does the annual reproductive potential remain the same, decrease or increase with age?
2. When does senility occur?
3. What is the ecological longevity?

C. What is the annual realized reproductive performance?

1. What is the annual period of reproductive activity in females? in males? What is the relation of this period to the total annual activity cycle?

   Baker (1947) discusses the causes of breeding seasons. Volsøe (1944) describes seasonal fluctuations in the reproductive system. Kendeigh (1941) summarizes information on the relation of length of day to gonad development. This period is usually considered as that period in which the females are "carrying" young or are laying eggs. Much confusion has resulted from failure to delimit this period. Thus it may be stated that a female having eggs in the oviduct was collected on a given date. Yet this is not clearly indicative of the time when eggs may be deposited. Each investigator should insure preciseness of definition. Writers frequently use the presence or absence of oviducal eggs to delimit the season but this can lead to potential errors if not weighed properly. Eggs may be retained in the oviducts for long periods (Cagle and Tihen, 1948).

2. What correlation is there between courtship or copulation and ovulation? What is the significance of the sex ratio and population density in relation to annual realized reproductive performance?

   These are little-explored areas in herpetology yet important ones if we are to arrive at an understanding of those factors controlling changes in reptile populations. The fact that some reptile females may bear young or deposit fertile eggs after as long as eight years after copulation suggests that unbalanced sex ratios may be of but scant consequence. The unverified yet not disproven statement that single or successive copulations are essential to stimulate ovulation indicates the importance of a favorable sex ratio. The work of Darling (1938), Vogt (1942), Errington (1946) and others has suggested that population density may markedly affect breeding success.

   a. What is the pattern of courtship?

      Exploration of the courtship patterns with emphasis on interspecies differences promises to yield much of value in explaining the development of physiological isolation. Noble and Bradley (1933) furnish many suggestions for procedure and interpretation. Cagle (1950) describes differences in the courtship pattern between two species of the genus *Pseudemys.* Davis (1936) summarizes the literature for snakes; Gloyd (1947) suggests additional problems; Greenberg (1945) summarizes the knowledge of courtship in the family *Iguanidae.*

    (1) How does it differ from that of related forms?
    (2) What advantages in reproduction are provided by the courtship pattern?
    (3) What selective factors function in courtship?
    (4) What secondary sex characters are of most significance in courtship?
    (5) What senses are involved in courtship? (Noble, 1937)

  b. What is the relation of courtship drives to aggregation? (Finneran, 1949).

  c. When do ovulation and fertilization occur?
    (1) What is the fertilization rate? The relation of successful courtship and copulation to fertilization rate?
    (2) Is copulation essential to ovulation? to egg depositions? (Woodward, 1933).

3. How many groups of young (eggs) are produced each year?

   This question must usually be answered by the examination of ovaries from chronological samples taken during the breeding season so that progressive changes in number and size of ovarian follicles or total volume or weight may be reported. Too, examinations of the ovaries of females at the end of the reproductive period may yield counts of ovulation points (corpus luteum or corpus albicans) (Samuel, 1952).

4. How many young (eggs) are produced in each group? Some investigators have depended solely upon counts of oviducal eggs or of eggs found in nests. Both procedures are subject to substantial error as the worker can but rarely be confident that no eggs have been previously deposited, that ovluation is completed or that two or more females have not utilized the same nest. Counts of ovulation points are usually more acceptable. Certainly the typical extreme variation in number of eggs and young produced emphasizes that little significance may be attached to many of

the literature reports of the number of young in single females or nests. Counts of young present in the uteri of viviparous or ovoviviparous forms possibly provide the most reliable criteria of clutch size. (The terms, viviparous and ovoviviparous, have been used in varied ways in herpetological literature. It is suggested that the term, ovoviviparous, be restricted to describe a situation in which the developing young gains no sustenance from the female).

a. Is there a correlation between reproductive capacity and size or age? How is this related to estimates of natality in local population?

The large difference in reproductive capacity between small and large females make it exceedingly difficult to utilize much of the published data on reproductive capacity as bases for estimates of natality.

VI. *What are the major factors controlling the relation of the number of surviving young to the number of eggs or young produced by females?*

A. What are the characteristics of the egg at deposition?

1. How do the eggs vary in size, volume and weight in each clutch?

The irregular shape of most reptile eggs reduces the value of measurements of length or width reported without volumes (Lynn and Brand, 1945).

2. Is there any correlation in size and/or weight and size of female?

3. What changes occur in size and weight of eggs during incubation?

The weight and volume of eggs change much and irregularly with age and the environment. Cunningham and Hurwitz (1936) reported that eggs increased as much as 60% in weight during incubation. Data on reptile eggs are of little value unless they are accompanied by statements as to their age and conditions under which they were incubated. The statistical treatment (Edgren, 1949) does not remedy this discrepancy.

4. In what stage of development is the egg at deposition?

a. Does this stage of development vary with the time eggs are retained in the oviducts? If so, how does this influence the incubation period?

b. How is the stage of development related to the egg size and weight?

B. Where and in what manner are eggs deposited?
   1. Is a nest constructed?
      a. What factors determine the nest site?
      b. How is the nest constructed?
      c. What is the relation of choice of nest site and construction to potential survival of young?
      d. What is the behavior pattern of the female constructing a nest? What features are of survival importance?
      e. Does the female use the same nesting site for subsequent clutches? in subsequent years?
   2. Does the female remain with the eggs? return to them? What is the relation of female behavior to survival potential of young? of the females?
      a. Does the female "defend" the eggs?
      b. Does the female contribute "heat" to incubation?

         These questions cannot be answered on the basis of single observations. Behavior of reptiles is sufficiently variable that repeated observations are essential to description of behavior patterns. In most situations the investigator can gain but restricted field data on these questions and is compelled to study captive specimens as a basis for evaluation of field-collected data (Noble and Mason, 1933).

C. What factors determine incubation rates?
   1. What is the period of incubation? in field nests? in the laboratory?
      a. What is the relation of temperature levels or changes to incubation time? of degree-hour to incubation time? (Cunningham, 1939).
      b. Are differences in incubation time between clutches of eggs related to egg-deposition (sequence in oviducts; time of retention in oviducts; quality of shell deposited)? Observers frequently do not state incubation periods in degree-hours and do not provide their criteria for "hatching". The extreme difficulty of evaluating much of the published material makes it unavailable for coherent treatment.

         It is not usually possible to observe the deposition of reptile eggs and the incubation period must be expressed as the interval between the laying of the last egg and the hatching of the last egg. This procedure is usually followed in reporting the incubation time of bird eggs (Skutch, 1950). Although reptiles typically deposit an entire brood over a short period as compared with birds, the total time required to deposit a brood is often significant in relation to the incubation period. The incubation time should be expressed in terms of days and hours or degree-hours.

2. How sensitive are eggs to low or high temperature during the incubation period? What extremes are the eggs subjected to in the typical nest site? Potential mortality?
3. How do the hatchlings escape from the egg? What is the function of the caruncle? What mortality is involved in the process of hatching?

D. Does the female develop any particular behavior traits associated with gestation?

1. What is the period of gestation? (Bragdon, 1951).
2. What are the principle causes of mortality during embryonic development?
3. Does the female tend to select a particular type of site for the birth of the young? Relation of such selection to potential survival?
4. Describe the birth of the young.

VII. *What are the characteristics of the young? Are there any typical behavior traits? What is the relation of the behavior pattern to survival? to growth?*

A. What advantageous resources in morphology, physiology, behavior patterns do the young adults possess? (Daniel and Smith, 1947).

1. What is the amount of yolk retained? Is it utilized as a source of nourishment? How long and under what conditions will it serve to support the young?
2. How long do the young remain in the nest or with the female? What factors influence the length of this period? May young overwinter in the nest? Remain with the female for prolonged periods? What relation may this bear to survival potentialities?

B. What are the major hazards to which the young are exposed immediately after leaving the nest or the female?

VIII. *What are the characteristics of the growth curve of individuals of the local population?*

A. What is the length of the growing season?

1. What are the factors serving to delimit the growing season? Availability of food? Changes in environmental temperature? Cyclic changes independent of temperature?

Various procedures have been attempted for determining the limits of the growing season. The actual observation of initiation and cessation of growth through study of seasonal samples is best but such observations are difficult to obtain. The correlation of formation of growth rings in turtles with season has been attempted (Cagle, 1946). Too, once the minimum and maximum effective temperatures of a form are known they may be utilized to approximate the time of initiation or slowing of activity. This does not, however, necessarily define the growing season as it has been demonstrated that reptiles may become quiescent during the winter although retained at constant temperature. Evans and Hegre (1940) have suggested that some genetic time factor, distinct from the temperature factor, is operative in reptiles.

2. What variations in length of growing season occur within the area of investigation?

   It is indicated by some researches that the time of initiation or cessation of growth may vary significantly from one local habitat or situation to another.

B. What is the annual increment (in that measure selected as the best indicator of total change in mass) during each season of the animal's life? What sex differences occur?

   1. What are the factors influencing the rate of growth? (size and/or age; senility, length of growing season, social dominance).
   2. What are the limits of variation in growth rates? How does growth rate affect the attainment of maturity, natality, mortality?
   3. What age or size groups may be discerned? (Klau and David, 1952).
   4. Is growth potentially continuous throughout the life of the individual?

C. What is the natural (ecological) longevity?

   1. What longevity records are available from captive sepcimens?
   2. What estimates of age may be made from the population samples (Woodbury, 1951).
   3. What are the characteristics of youth, maturity, old age?

IX. *What is the annual cycle of activity and what factors exert primary influence on the cycle?* (Fitch and Glading, 1947; Oliver, 1947).

A. What is the relation of the growing season to the period (periods) of courtship, egg-deposition and birth of young?

B. What are the optimum, minimum and maximum effective body temperatures?

C. What is the seasonal cycle in diel behavior (e.g., in basking) (Girons, 1947).

D. Are the animals quiescent during any period of the year? Are aggregations formed?

  1. What preparations are made for the period of quiescence?
  2. Where do the animals spend the winter?
  3. What environmental factors cause the initiation of quiescence? renewed activity?

     Bailey (1949) demonstrated that the plains gartersnake, *Thamnophis radix* could endure temperatures of approximately —2°C. for a protracted period.
  4. What is the composition (age groups, size groups, sex ratios) of the winter aggregation?
  5. What is the role of winter quiescence in limiting the geographic distribution? (Bailey, 1948).

X. *What is the diel cycle of activity?*

A. What is the role of basking in the daily cycle?

  1. What determines the time of basking, the length of the period?

     Sergeev (1939) reports a close relation between environmental temperature and the period of activity. Benedict (1932) summarizes temperature relations in reptiles.
  2. What is the function of basking?
     a. How is the period of basking related to rate of increase or decrease of body temperature?
     b. What is the characteristic behavior pattern in basking. How is this related to control of body temperature? (Cowles and Bogert, 1944; Gunn, 1942; Chernomordikov, 1943; Bogert, 1949).

B. Is feeding restricted to any particular part of the day? How is the feeding behavior or length of the feeding period influenced by food availability?

C. Are breeding activities (courtship; egg-deposition; birth of young) restricted to any part of the day?

D. When does the peak of activity occur in the daily cycle?

E. How is the diel (Klauber, 1939) cycle modified by weather changes, population density?

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Interspecies differences in the diel cycle of activity may affect the entire life history. Exploration of the cycle may yield the key to many of the problems presented here. Noble (1946) presents valuable information on such problems.

XI. *What are the food habits? Their relation to growth and survival?*

- A. How does the animal obtain its food?
  - 1. Can the animal pursue and catch actively moving prey?
  - 2. What food preferences are exhibited in the field and laboratory?
- B. What are the principle foods? Relation to availability?
  - 1. What is the relative importance of the food items?
  - 2. How do feeding habits vary during the life of the animal?
  - 3. Is there any seasonal variation in feeding habits?

    Most studies of reptile food habits have reported a high percentage of empty stomachs. It is thus essential that the investigator utilize intestinal as well as stomach contents. Too, the fecal material of many reptiles may be used. Fitch and Twining (1946) emphasize the value of scats in the determination of the food habits of snakes. The scats of lizards, particularly, are of great value in food analysis. Carpenter (1952) obtained data on food habits of snakes by forcing regurgitation. Lagler (1943b) reviews the food habits of Michigan turtles.
- C. Does the animal act as a controlling or limiting predator?

XII. *Does this form exhibit any characteristic and genetically limited patterns of group behavior?*

The study of behavior under undisturbed natural conditions often yields startling information of basic importance to the explanation of population problems (Svärdson, 1949; Calhoun, 1950; Carpenter, 1950) and phylogeny (Bellairs and Underwood, 1951). Few zoologists have developed the ability to profit from the observation of field behavior patterns (Emlen, 1950). Herpetologists, particularly have not utilized this procedure.

- A. Do aggregations occur? If so what are the stimuli and binding forces in aggregation? the function of the aggregation? (Noble, 1936; Allee, 1931, 1951; Greenberg, 1943.)
- B. Are social hierarchies present?
  - 1. If dominance hierarchy is present, what is the relation

to territoriality, natality? (Evans, 1938, 1951; Greenberg, 1943).

2. How does the social hierarchy affect the migrating individual? the juvenile seeking a territory?
3. Does the social hierarchy influence growth and reproductive potential? (Calhoun, 1950).

   Such questions as these may be answered if some of the methods of field ornithologists be adapted. The use of blinds and optical equipment for observation will yield much of value to the interpretation of interactions. Observation towers were used to study the behavior of turtles in Illinois (Cagle, 1944; 1950). Excellent suggestions, many of which are of value to the herpetologist, are presented by Emlen (1950). The work of Evans (1938, 1951) is suggestive of problems and procedures.

C. Are there typical defensive or offensive behavior patterns? Bogert (1941) describes the "king-snake defense posture" of rattlesnakes. Mertens (1946) summarizes reports of such actions in reptiles.

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Contents

Editorials

Invited Forums

HerpSpectives

Research Articles

Classics in HCB

Inside this issue: Observing amphibians and reptiles does not always involve turning rocks. Here, Steve Sillett examines a large limb in the crown of the largest known redwood in search of *Aneides vagrans*, Jedediah Smith Redwoods State Park, California. (Photographed by Marie Antoine, compliments of Steve Sillett).

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