

Dr. Thibodeaux promptly called Whit and told him to stop me from pursuing the topic. He claimed that this was his idea, and he intended to work on it sometime in the indefinable future. Whit expressed his support for whatever I wanted to do, but I ended up changing dissertation topics. Little did I realize, however, that I would run into the same situation with another respected authority from a different field. Submission of my dissertation work for publication (Camp 1988) prompted a letter from Dr. Erhöhung (again, a pseudonym), who happened to serve as a reviewer for the journal. Dr. Erhöhung essentially told me to cease and desist from all work in this area as it competed with part of a broader study that he was conducting. He noted that he had earlier published a statement of intent concerning his study and, therefore, no one else had any right working on it. More recently, this same researcher has used his influence to get a major, publicly funded museum to deny me access to specimens for the same stated reason. Considering these personal experiences, I have no doubt that similarly minded researchers may use their influence to prevent “threatening” papers from getting published. I would hope, however, that this ploy succeeds only rarely.

I suspect that few researchers actually have the clout to prevent others from working in “their area.” More commonly, perceived encroachment simply generates hard feelings, with the unfortunate consequence of preventing meaningful collaboration. On the other side of the same coin, I know researchers who avoid working on certain topics or even reviewing related manuscripts for fear of stepping on someone’s toes. I do not know if this mindset of first-come, first-research is unique to herpetology, but other scientific disciplines seem rife with competitive research, as rival labs race for the accolades of scientific discovery.

Although herpetology may seem enviable with its ordered, friendly, even chivalrous approach to doling out research areas, the result is to stymie scientific advancement. Platt (1964) argued that science successfully proceeds by testing competing, alternative hypotheses. The effective stillbirth of such hypotheses through the exclusion of other minds translates into a *status quo* that retreads the same old stale ideas and stifles intellectual headway. I believe that this attitude has, at least in part, contributed to a “lack of novel hypotheses” (Tilley and Bernardo 1993) in certain areas of herpetology. Moreover, the confirmation of conclusions through the replication of results is an important, albeit often overlooked cog in the engine of scientific progress.

It is particularly disheartening when established researchers, whose careers have already been made, expect new, budding scientists (i.e., graduate students) to tug their forelocks in deference and meekly shuffle off to find something else to work on. This sends, if not exactly a stake through the heart of science, certainly a thorn into its flesh. After all, it is not the old dogs that create new, revolutionary ideas, but it is those who are “almost always...either very young or very new to the field....who, being little committed by prior practice to the traditional rules of normal science, are particularly likely to see that those rules no longer define a playable game and to conceive another set that can replace them” (Kuhn 1970).

We are all human, and none of us likes the thought of being scooped. I fully understand the annoyance resulting from a discussion with a young colleague that inadvertently creates a competitor. Even so, competition sharpens us as scientists, and the

fear of it does not legitimize claims of ownership. Planting one’s flag, so to speak, in certain research topics or taxonomic groups is nothing short of intellectual imperialism. Protecting research turf may contribute to legacy-construction, but science is driven by ideas, not legacies. Science in general, and herpetology in particular, benefits by putting personal claims aside. My advice to those who wish to avoid being scooped is to simply work faster. To those considering research projects in “pre-owned” areas, go ahead. Rather than deferring to the authorities, send them reprints.

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POINTS OF VIEW

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Snake Relationships and Ambiguous Data

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Dowling et al. (1996) used allozyme data from four protein loci to infer higher level snake phylogeny. Their conclusions were based on a single tree inferred using UPGMA clustering. Buckley et al. (2000) reanalyzed the allozyme data of Dowling et al. (1996), discovering numerous identical distance values between pairs of taxa and therefore the existence of numerous equivalent UPGMA trees. Based on more thorough tree searches using UPGMA clustering, minimum evolution, and parsimony analysis, they concluded that the data in question were highly ambiguous concerning the higher level phylogeny of snakes, and that the high degree of resolution in the tree of Dowling et al. (1996) was an artifact produced by selecting one out of many equivalent trees.

Highton et al. (2002) responded by questioning three of the practices used by Buckley et al. (2000) to reach their (our)

conclusions: 1) our exclusion of OTUs with allelic complements (and therefore genetic distances) identical to those of other OTUs in the distance matrix, 2) our use of a single taxon input order rather than multiple randomized input orders of taxa, and 3) our use of the strict consensus method rather than the majority-rule consensus method. The overall suggestion was that, when these three supposed problems are corrected, the data in question yield a high degree of phylogenetic resolution. That conclusion is unfounded, as we here demonstrate by addressing the three criticisms.

It should be noted that although Highton et al. (2002) stated that their original study was aimed primarily at lower level relationships, Dowling et al. (1996) nevertheless presented a tree that had considerable resolution regarding deep branches and called attention to the existence of 18 major groups and their inter-relationships (see their Fig. 6). Furthermore, the somewhat less resolved tree defended by Highton et al. (2002) still exhibits considerable deep resolution. Thus, the issue remains whether the data of Dowling et al. (1996) support the level of resolution in the tree presented by Highton et al. (2002) as opposed to the much lower levels of resolution in the results of Buckley et al. (2000).

1. EXCLUSION OF IDENTICAL TAXA

One of the reasons that Highton et al. (2002) obtained greater resolution than we did for the same data was that they retained taxa with identical alleles at all four loci that they surveyed. Buckley et al. (2000) removed identical taxa prior to analysis because such taxa provide no additional information about the structure of the tree (i.e., beyond the fact that they will always cluster with the taxa to which they are identical). According to Highton et al. (2002:720), "Actually, adding or deleting identical taxa may affect tree topology. If identical OTUs are removed from a study, the remaining OTUs may join more basal branches in a different order." Although they are correct in stating that removing identical taxa can affect tree topology, at least for some methods (see below), and although we overlooked the fact that this property holds for UPGMA clustering, we maintain that the sensitivity of that method to the presence or absence of identical taxa is an undesirable property. The resolution resulting from it in the trees of Dowling et al. (1996) and Highton et al. (2002) is therefore unwarranted.

Consider the example of *Amphiesma stolata*, *Clonophis kirtlandi* and various taxa with identical alleles at all four loci, *Sinonatrix annularis*, *Regina rigida*, and *R. septemvittata*. In our UPGMA consensus tree (Buckley et al. 2000:Fig. 1), based on an analysis that excluded the taxa identical to *Clonophis*, each of these taxa forms a separate branch of a large polytomy made up of 73 branches, three nodes above the root of the tree. This situation reflects the fact that several of the species in question exhibit distances of 0.5000 or (in one case) 0.7500 to one another, which are equal to or greater than distances between these species and other species making up other branches of the polytomy, in particular, those making up a group composed of species of *Rhabdophis* and *Xenochrophis*. In contrast, in the majority rule consensus tree of Highton et al. (2002:Fig. 1), the species of *Amphiesma*, *Clonophis* and identical taxa, *Sinonatrix*, and the two species of *Regina* form a resolved group, and moreover, that group is resolved as being most closely related to the group composed of *Rhabdophis* and *Xenochrophis* species.

These discrepancies result from the inclusion versus exclusion of identical taxa in combination with the properties of UPGMA clustering. UPGMA is an average linkage clustering method (Sneath and Sokal 1973). It operates by iteratively forming groups made up of pairs of taxa (OTUs), or of previously formed groups, based on the average distances between their member OTUs. As the name indicates, UPGMA uses an unweighted averaging procedure. This means that when OTUs or groups of OTUs are united to form an initial or larger group, the average distance between this new group and all other OTUs or groups (which is needed to determine which group to unite in the next iteration of the procedure) is calculated by taking the arithmetic mean (average) of all of the relevant pairwise distances between the individual OTUs as present in the original (unclustered) matrix. This "unweighted" averaging procedure has the effect of weighting all comparisons equally and can be contrasted with the weighted averaging procedure used in a related method known as WPGMA. In weighted averaging, the average distance between a group and all other OTUs or groups is calculated by taking the average of the pairwise distances, not between individual OTUs in the original matrix, but between the two groups of OTUs in the matrix used in the previous iteration of the procedure. For example, suppose a previously formed group composed of *Clonophis kirtlandi* and *Sinonatrix annularis* is united to form a larger group with *Regina septemvittata*. With unweighted averaging, the distance from the group composed of these three species to *Regina rigida* will be calculated as the average of the distances between *C. kirtlandi* and *R. rigida*, *S. annularis* and *R. rigida*, and *R. septemvittata* and *R. rigida* = $(0.5000 + 0.5000 + 0.2500)/3 = 0.4166$. In contrast, with weighted averaging, the distance from the group of three species to *R. rigida* will be calculated as the average of the distance between the group *C. kirtlandi* + *S. annularis* and *R. rigida* (calculated in the previous iteration of the procedure) and that between *R. septemvittata* and *R. rigida* = $(0.5000 + 0.2500)/2 = 0.3750$.

Because of the properties of unweighted averaging, it should be clear that the inclusion of identical taxa can indeed affect the results of UPGMA clustering (but should not affect those of WPGMA clustering). Thus, using the same example, if taxa with identical alleles to those found in *Clonophis kirtlandi* are included in the analysis, then these taxa will always cluster with *Clonophis* before either they or *Clonophis* clusters with other taxa, and therefore, the distance between any OTU or cluster and one containing *Clonophis* and these identical taxa will be affected by the inclusion (and number) of the identical taxa. Specifically, when taxa identical to *Clonophis* are excluded, *Amphiesma stolata* clusters with *Rhabdophis* and *Xenochrophis* rather than with *Clonophis*, *Sinonatrix* and *Regina* in some of the identical UPGMA trees, reflecting the fact that *A. stolata* exhibits distances to the former taxa (0.5000) that are as small or smaller than those that it exhibits to some of the latter taxa (0.5000–0.7500). However, if even one taxon identical to *Clonophis* is included, then the average distance from *Amphiesma* to any group containing *Clonophis* and identical taxa is decreased, and *Amphiesma* always clusters with one or more of *Clonophis*, *Sinonatrix*, and *Regina* before it clusters with *Rhabdophis* and *Xenochrophis*, despite the fact that some of the distances between *Amphiesma* and the former taxa (0.5000–0.7500) are as large or larger than those that it exhibits to the latter taxa

(0.5000). Such resolution is not warranted by the data, and this situation suggests that either the identical taxa should be excluded or, if they are to be included, that WPGMA rather than UPGMA clustering should be used.

2. TAXON INPUT ORDER

Highton et al. (2002) are correct in their assertion that randomization of the input order of taxa can be used to break ties. However, they are incorrect in stating that “Buckley et al. (2000) reached their conclusions [i.e., about lack of resolution] because they used only strict consensus trees and did not randomize the order of their input taxa” (p. 270). In fact, the procedure of randomizing taxon input order is functionally equivalent to the systematic (NTSYS) and random (PAUP) tie-breaking procedures used by Buckley et al. (2000). All of these methods cause the clustering procedure to follow different pathways in the case of tied-values, and consequently, they produce different, but equivalent, trees. The main differences are that all possible pathways are taken in the case of systematic tie-breaking, while (usually) different random pathways are taken in the case of random tie-breaking and randomizing taxon input order. Therefore, the greater resolution in the consensus tree of Highton et al. (2002:Fig. 1) relative to that of Buckley et al. (2000:Fig. 2) results from the difference in consensus methods (see below) and the fact that Highton et al. (2002) examined only 50 of the many equivalent trees, compared to the 9999 (systematic tie-breaking) and 1000 (random tie-breaking) equivalent trees examined by Buckley et al. (2000).

It should be noted that Highton et al.’s discussion of the relationships among *Carphophis*, *Diadophis*, and *Farancia*, which they used to argue that we should have used different random input orders of taxa, is confused. They correctly pointed out that the UPGMA tree of Dowling et al. (1996:Fig. 3) and the strict consensus of the 9999 UPGMA trees of Buckley et al. (2000:Fig. 2) both have the relationships ((*Carphophis*, (*Diadophis*, *Farancia*)), and this is also true for the majority rule consensus of the 50 UPGMA trees of Highton et al. (2002:Fig. 1). However, they incorrectly stated that “In [Buckley et al.’s] Fig. 3, their 9999 trees all had a different topology ((*Carphophis*, *Diadophis*), *Farancia*) indicating the input order had been reversed” (Highton et al. 2002:271). On the contrary, Fig. 3 of Buckley et al. is not the consensus of 9999 UPGMA trees but of six minimum evolution (ME) trees, with branches less than 0.0646 (the smallest observed value) collapsed. For our ME analysis, we used the same input order of taxa as for our UPGMA analyses. Therefore, the difference between our ME consensus tree and the various UPGMA consensus trees presumably results from the different method used for that analysis.

In contrast with UPGMA, the ME method does not assume (approximate) evolutionary rate equality among lineages. This property is important in the case of the three taxa in question, because although *Carphophis* exhibits a greater distance to *Diadophis* (0.3571) and *Farancia* (0.5991) than those taxa do to each other (0.3318), the *Carphophis* and *Diadophis* lineages appear to be evolving rapidly for the set of loci sampled, relative to the *Farancia* lineage. Assuming that these three taxa form a monophyletic group (as suggested by both the UPGMA and ME but not the parsimony analyses of Buckley et al. 2000), relative

rate tests using *Calamaria gervasii* and *Rhamphiophis oxyrhynchus* (taxa that share the most alleles with *Carphophis*, *Diadophis*, and *Farancia*) as outgroups, reveals substantially greater distances to *Carphophis* and *Diadophis* ($D = 0.8664 - 0.9286$) than to *Farancia* ($D = 0.5000 - 0.5991$). Consequently, even though *Diadophis* is more similar to *Farancia* than to *Carphophis* (for the loci in question), as indicated by the results of the UPGMA analysis, it may share a more recent common ancestor with *Carphophis* than with *Farancia*, as indicated by the results of the ME analysis.

The pattern of shared alleles supports this interpretation. At the only locus (*Acp*) for which *Diadophis* and *Farancia* share an allele (24) not found in *Carphophis*, the allele in *Carphophis* (31) is unique to that taxon (among all snakes examined) and is therefore potentially autapomorphic. In other words, the allele shared by *Diadophis* and *Farancia* may be ancestral for all three taxa, and consequently, the fact that it is shared by *Diadophis* and *Farancia* does not support a relationship between those taxa to the exclusion of *Carphophis*. In contrast, *Carphophis* and *Diadophis* share an allele (07) at the *Mdh* locus that appears to be derived relative to the allele (06) present in *Farancia* (based on presence of allele 06 in other snake species), suggesting that *Carphophis* and *Diadophis* share a common ancestor not shared by *Farancia*.

Highton et al. (p. 271) reached their erroneous conclusion about taxon input order because they believed that “the *I*-value between the pair *Carphophis* and *Diadophis* is the same as that between *Diadophis* and *Farancia*” and “the tie was no longer present [in the majority rule consensus tree of Highton et al.] because [they] included two species of *Farancia*.” On the contrary, the *I* value for the *Carphophis*-*Diadophis* comparison ($I = 0.6429$; $D = 0.3571$) is not the same as that for the *Diadophis* -*Farancia* comparison ($I = 0.6682$; $D = 0.3318$), reflecting the fact that the allele shared by *Carphophis* and *Diadophis* at the *Pgm* locus (08) is polymorphic in both taxa, while that shared by *Diadophis* and *Farancia* (also 08) is polymorphic in *Diadophis* but not in *Farancia* (both pairs of taxa share all their alleles at two of the other three loci and none at the third). Thus, the clustering of *Diadophis* with *Farancia* in the various UPGMA analyses has nothing to do with including two species of *Farancia*. Because the distance between those two taxa is smaller ($D = 0.3318$) than the distance between *Carphophis* and *Diadophis* ($D = 0.3571$) and that between *Carphophis* and *Farancia* ($D = 0.5991$), *Diadophis* and *Farancia* cluster together in all the various UPGMA analyses—both those excluding (Buckley et al. 2000:Fig. 2) and those including (Highton et al. 2002:Fig. 1) the second species of *Farancia*. (The same is true for the Cavalli-Sforza and Edwards chord distances used by Highton et al., which are 0.0383, 0.0444, and 0.0679, respectively.)

3. CONSENSUS METHODS

The suggestion by Highton et al. (2002) that we overlooked the phylogenetic signal present in the data of Dowling et al. (1996) by using the strict consensus method rather than the majority-rule consensus method highlights the general problem of deciding which groups are to be considered supported by the results of a phylogenetic analysis. Consensus methods, of which several have been proposed (reviewed by Swofford 1991; Nixon and Carpenter 1996), bear on this question in that they are commonly used to assess agreement among the members of a set of equivalent trees. The strict consensus method (Schuh and Polhemus 1981) used by

Buckley et al. (2000) retains only those groups that appear on all trees in the set. In contrast, the majority-rule consensus method (Margush and McMorris 1981) advocated by Highton et al. (2002) retains all groups that are present in some arbitrarily specified proportion of the trees greater than or equal to 50%. Other less-than-strict methods (e.g., reduced consensus, Adams consensus) also seek to retain more resolution, but this increased resolution is accomplished at the expense of ignoring contradictory data (Kearney 2002; Nixon and Carpenter 1996).

Choice of a consensus method reflects the stringency of the standard of group support adopted. Within this framework, various standards of group support form a continuum ranging from least rigorous to most rigorous as follows: any character support at all → present on any of the optimal trees → present on a majority (>50%) of the optimal trees (the criterion adopted by Highton et al. 2002) → present on various fractions of the optimal trees above 50% → present on all (100%) of the optimal trees (the criterion adopted by Buckley et al. 2000) → present on a majority (> 50%) of the optimal trees resulting from bootstrap/jackknife analysis (this criterion will not always be more stringent than the preceding one because it is based on a qualitatively different property) → present on various fractions above 50% of the trees resulting from bootstrap/jackknife analysis (commonly used fractions are 70%, 90%, and 95%).

In this context, Highton et al. (2002) advocated a consensus method (50% majority-rule) that resides near the permissive end of the spectrum, whereas Buckley et al. (2000) used one (strict or 100% majority rule) that corresponds with a more stringent criterion. As a result, Highton et al.'s (2002) consensus tree contains groups that are contradicted by some of their equivalent trees, whereas Buckley et al.'s (2000) consensus tree contains only those groups that are not contradicted by any of their equivalent trees. Although authors are free to adopt as permissive or stringent a criterion as they see fit, the recent trend in phylogenetics has been to use much more stringent criteria than the one adopted by Highton et al. (2002). Thus, the strict consensus method is the most commonly used consensus method for representing agreement among equivalent optimal trees resulting from a single phylogenetic analysis (Nixon and Carpenter 1996; Swofford 1991), and many recent authors demand even more stringent criteria for considering a group to be adequately supported, such as presence in 70% or even 95% of the optimal trees obtained using bootstrap or jackknife resampling methods.

We performed bootstrap analyses, each with 100 replicates, using the phylogenetic software packages PAUP* version 4.0b10 (Swofford 2002), for UPGMA and parsimony analyses, and FastME (Desper and Gascuel 2002), for minimum evolution analyses, to assess levels of support provided by the allozyme data for various groups of taxa. Following the program default, we considered presence of a group in 50% of the bootstrap replicates to be the minimum level of acceptable support (given that a group present in less than 50% of the replicates can be contradicted in more replicates than it is supported). The original published tree of Dowling et al. (1996) has 122 groups (nodes), or 103 excluding those composed of taxa with identical character states; the majority rule consensus tree of Highton et al. (2002) has 105 groups, or 86 excluding those composed of identical taxa. By comparison, bootstrap analysis using UPGMA yielded only 18 and 8 groups

(total and excluding those composed entirely of identical taxa) supported in greater than 50% of the replicates; bootstrap analysis using minimum-evolution yielded only 40 and 19 groups; and bootstrap analysis using parsimony analysis yielded 0 groups.

In sum, the majority-rule consensus tree presented by Highton et al. (2002) corresponds with a relatively permissive criterion of support (presence in > 50% of the equivalent trees) in that it retains groups that are contradicted by some of the equivalent trees. Under more stringent criteria that are widely adopted by contemporary workers (presence in all of the optimal trees; presence in greater than 50% of the trees resulting from bootstrap analysis), considerably less resolution is obtained. Moreover, the UPGMA clustering method used by Highton et al. (2002) carries an unrealistic assumption of evolutionary rate constancy among lineages (de Queiroz and Good 1997, and references therein), and at least some alternative methods yield even less resolution and/or contradictory groupings (e.g., the relationships among *Carphophis*, *Diadophis*, and *Farancia*) for the allozyme data in question (Buckley et al. 2000).

Conclusion.—Rather than contradicting the conclusions of Buckley et al. (2000), the results presented by Highton et al. (2002) reinforce those conclusions. Although Highton et al. (2002) are correct in stating that the removal of identical taxa can affect the order of clustering by UPGMA, any increased resolution that results from including identical taxa is not warranted by the data in that it is an artifact of sampling and the averaging method used by UPGMA. Highton et al. (2002) are incorrect in stating that if we were interested in the effects of ties on the topology of UPGMA trees based on the snake allozyme data, we should have randomly reordered the input of taxa. In fact, the tie-breaking procedures that we used are equivalent to varying the input order of taxa, and we performed much more thorough tie-breaking analyses than did Highton et al. (2002) (our analyses effectively used 20 to ~200 times the number of different input orders used by them). Finally, Highton et al. (2002) used a very permissive criterion (majority-rule consensus) for deciding which nodes to consider resolved. A more conservative and widely used criterion (strict consensus) results in far less resolution (particularly when more thorough tie-breaking analyses are performed), and a standard method for assessing nodal support indicates that most of those nodes are very weakly supported.

For these reasons, our conclusions remain unchanged. The snake allozyme data of Dowling et al. (1996) are highly ambiguous concerning the higher level phylogeny of snakes, though they may be informative at lower hierarchical levels. The high degree of resolution in the original tree of Dowling et al. (1996: Figs. 1–6) is an analytical artifact that results from failure to consider alternative trees implied by numerous tied distance values. In addition, the new tree presented by Highton et al. (2002: Fig. 1), though less resolved than the one presented by Dowling et al. (1996), still contains more resolution than is warranted by the data. Many of the groups in that tree result from 1) retaining identical taxa in conjunction with use of a tree reconstruction method (UPGMA) that is sensitive to the numbers of identical taxa sampled, 2) performing a less than thorough tie-breaking analysis, and 3) using a permissive consensus method (majority-rule) that allows contradicted groups to be retained in the summary tree.

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ARTICLES

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Reproductive Arrest in *Sceloporus mucronatus* (Lacertilia:Phrynosomatidae) Correlated with “El Niño Southern Oscillation”

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The most common reproductive patterns in *Sceloporus* lizards that inhabit temperate and high mountain zones in central Mexico are viviparity and fall reproduction (Guillette and Méndez de la Cruz 1993; Méndez-de la Cruz et al. 1998). Indeed, all species of the *torquatus* group (*S. jarrovi*, *S. cyanogenys*, *S. mucronatus*, *S. torquatus*, *S. poinsetti*, *S. dugesi*, and *S. serrifer*) that have been studied exhibit fall ovulation and spring parturition following 5 to 7 months of gestation (Méndez-de la Cruz et al. 1998). Previous studies of these species have shown that one litter per year is char-

acteristic, but that parturition might be delayed by less than one month (Guillette and Méndez-de la Cruz 1993; Méndez-de la Cruz et al. 1998).

Clutch size is an adaptation to abiotic and biotic environmental factors and is an important reproductive trait of lizards (Fitch 1985). In general, lizards produce at least one clutch per year, but clutch size might vary within a population from year to year (Abell 1999; De Marco 1989). Desert lizards might reduce egg production in response to low precipitation as described for several species of *Uma* (Mayhew 1965; 1966a; 1966b), *Urosaurus ornatus* (Martin 1977), and *Uta stansburiana* (Worthington 1982). Reproduction was totally curtailed in *Cnemidophorus tigris* (Pianka 1970) and *Sauromalus obesus* (Nagy 1973) when extremely dry conditions reduced food resources.

We suggest that the reported reproductive failure in *C. tigris* and *S. obesus* was associated with the climate phenomenon called “El Niño Southern Oscillation” (ENSO). This event is the result of unusual periodically occurring sea surface temperature conditions in the eastern tropical Pacific Ocean that have global climatic effects (Trenberth 1997). During the last 50 years, 12 ENSO events have been recorded; the most severe event in Mexico occurred during 1997–1998 (Magaña and Morales 1999).

Our study of the viviparous lizard *Sceloporus mucronatus*, which inhabits the high altitude zone of central Mexico, was carried out during three consecutive years (1996–1998) in the same outcrop. The study area was located near Zoquiapan, Estado de México (19°20'04"N, 98°42'49"W). Twenty-eight females were randomly collected from crevices in rocks by hand, noose, or by using a wire to force a lizard from its refuge. Lizards were captured in May and June, prior to parturition. Lizards were housed for approximately one month in terraria with food and water *ad libitum* until the beginning of parturition, which is marked by sinuous abdominal contractions as previously described by Cuellar (1984). Data obtained from each female were snout–vent length (SVL to 1 mm) and total body mass (TBM) plus litter weight (to 0.1 g). After parturition, litter size and litter mass per female were determined.

For years with offspring production, we statistically compared litter size (LS), litter mass (LM), individual litter mass (ILM), female SVL, and female mass by year using t-tests. ANCOVA was used to compare female TBM from all three years, using SVL as a covariate, and year as a factor. ANCOVA was also used to compare the litter size of this population with different populations described in a previous study (Méndez-de la Cruz et al. 1993), using SVL as a covariate and study as a factor. Data were analyzed using SYSTAT. A significance criterion of $p \leq 0.05$ was used for all statistical analyses. Means \pm 1 SE are reported.

The twelve adult females collected during 1996 and 1997 were all gravid, and the t-test for LS, LM, ILM, and female SVL and TBM showed no significant difference between years ($t_{LT} = 0.93$, $P = 0.19$; $t_{LM} = 0.70$, $P = 0.25$; $t_{ILM} = 0.044$, $P = 0.33$; $t_{SVL} = 1.23$, $P = 0.13$; $t_{TBM} = 1.86$, $P = 0.07$). However, during 1998, none of the sixteen females collected was gravid, and no neonates were seen in the field. Females collected in 1998 were significantly different from the 1996–1997 females. The ANCOVA between body mass and year using SVL as a covariate showed significant differences between 1998 and 1996–1997, but not within 1996–1997 ($F_{1,2} = 19.09$; $P = 0.0001$). SVL and TBM for reproductive fe-