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Phylogenetic and Adaptive Variation in Lizard Femoral Gland Secretions

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The protein compositions of femoral gland secretions from 16 lizard species was compared using polyacrylamide gel electrophoresis. Similarities between species were examined both with a reciprocal averaging ordination that grouped species according to secretion similarity, and using trees constructed by the Wagner parsimony method. Closely related species have secretions that are more similar than more distantly related species, although not all of the interspecific variation in secretion chemistry can be explained by phylogeny. Intraspecific variation in the secretions of *Iguana iguana* and *Dipsosaurus dorsalis* indicates that femoral gland secretions could be used in individual and sex recognition.

VARIATION both within and between species in the chemical composition of pheromone signals has been documented in many communication systems (Wilson, 1970; Albone, 1984; Brown and MacDonald, 1985). While species-specificity in secretion composition is widespread, species with shared phylogenetic histories often possess pheromones of similar,

though not identical, chemical structure (Roe-lofs, 1979; Stoddart, 1980; Bell and Cardé, 1984). Concordance in pheromone structure among closely related species is potentially the result of two factors. Species that are close phylogenetically may share more pheromone components because they are descended from a common ancestor that possessed those components. Under these circumstances, pheromone composition may not represent adaptation to present ecological conditions, but may instead reflect retention of a trait that evolved in past environments (Gould and Vrba, 1982; Lauder, 1982; Dobson, 1985).

An alternative factor influencing secretion composition is adaptation to extant ecological conditions. The chemical composition of a pheromone in part determines its physical properties, including the maximum distance it travels, how quickly it spreads, how long it lasts, and how much information it encodes (Bossert and Wilson, 1963). Because environmental factors such as temperature, humidity, and substrate type affect the volatility and stability of most chemicals (Regnier and Goodwin, 1977), they can influence the spatial and temporal parameters of pheromone transmission. Thus, chemical compounds that differ in structure are not expected to be equally useful for pheromonal function in different environments. Species having similar ecologies may produce pheromones with common components because those particular components serve their functions well under current environmental conditions.

Superimposed on interspecific variation in secretion composition is an additional component of variation due to differences between individuals within a species. Intraspecific variation in pheromone composition may be significant at several levels: between kin groups, the two sexes, different age classes, and individuals within the same kin, sex, and age class (Stoddart, 1980; Bell and Cardé, 1984). Assessment of variability in secretion composition among species should consider these potential sources of intraspecific variation in addition to historical and ecological components of interspecific variation. Although phylogeny and ecology are often confounded when comparing evolutionary trends across taxa, statistical methods for assessing the independent influence of each have been developed (Harvey and Mace, 1982; Felsenstein, 1985; Bell, 1989).

Many lizards possess femoral glands on the ventral surface of the hindlegs (Cole, 1966;

Maderson, 1972). The glands, which are under the control of androgenic hormones (Chiu et al., 1970, 1975; Fergusson et al., 1985), usually are more developed in males than in females and are most active during the breeding season (Cole, 1966). The glandular exudate contains lipids (Alberts, 1990; Weldon et al., 1990) and proteins (Cole, 1966; Fergusson et al., 1985; Alberts, 1990). The classes of lipids present in femoral gland secretions appear not to vary between the sexes in *Dipsosaurus dorsalis* (Alberts, 1989b) and *Amphibolurus fordi* (Cogger, 1978), or between adult and juvenile males in *Iguana iguana* (Weldon et al., 1990), but the possibility that individual lipid components within those classes differ in identity or concentration with sex or age remains to be examined. The high protein content of the secretions indicates that they are probably energetically expensive to produce, and, together with cyclic and sexually dimorphic activity, strongly suggests that the glands are not vestigial (Cole, 1966; Alberts, 1990).

Although their specific communicative function may differ across species, it is probable that the lipid and protein components of femoral gland secretions, either separately or synergistically, act as pheromone signals. Lipids are prevalent in the chemical communication systems of many organisms (Hadley, 1985), including reptiles (Garstka and Crews, 1981; Cooper and Garstka, 1987). Proteins, which are likely to be detectable to lizards either through gustation (Beidler, 1977; Schwenk, 1985) or vomeronasal olfaction (Burghardt, 1970; Parsons, 1970; Halpern, 1987), may also transmit chemical information, or they may serve as a matrix to retard evaporation of lipids. Femoral gland secretions elicit elevated levels of tongue-flicking compared to controls in the iguanids *Sceloporus occidentalis* (Duvall, 1986) and *Dipsosaurus dorsalis* (Alberts, 1989a). Although the precise function of femoral gland secretions remains unknown, in *D. dorsalis*, they probably are used in conspecific recognition and may function in home range marking (Alberts, 1989b).

Because femoral glands occur in lizard families with divergent ecologies (Smith, 1946), they provide a promising model for investigating the relative importance of historical and ecological influences on interspecific variation in secretion composition. In this study, I examined the protein composition of femoral gland secretions of 16 lizard species that span a range of phyloge-

netic and ecological similarity, and evaluated the relative roles of historical and adaptive processes in the evolution of secretion chemistry. For two of the species, I also quantified intraspecific variation in protein composition.

MATERIALS AND METHODS

Secretion collections.—Femoral gland secretions were obtained from the following sources: 1) *Dipsosaurus dorsalis*, *Urosaurus graciosus*, *Phrynosoma platyrhinos*, *Gambelia wislizenii*, *Sceloporus orcutti*, and *Cnemidophorus tigris* caught in the Coachella Valley, Riverside County, California (CA); 2) *Sceloporus occidentalis* and *Uta stansburiana* noosed on the University of California, San Diego campus; 3) *Brachylophus vitiensis* caught on Macuata Island, Fiji; 4) *Brachylophus fasciatus*, *Iguana iguana*, *Sauromalus obesus*, and *Petrosaurus thalassinus* at the San Diego Zoo; 5) *Gerrhosaurus major* at the Living Desert Reserve in Palm Desert, CA; and 6) *Petrosaurus mearnsi* and *Urosaurus microscutatus* at the University of California Boyd Deep Canyon Desert Research Center in Palm Desert, CA. All samples represent secretions from a single adult male, except for the sample from *B. vitiensis*, which was obtained from an adult female. For *I. iguana* and *D. dorsalis*, secretions were collected from five males, and six males and three females, respectively. All samples were obtained during Spring, 1988.

Secretions were collected by applying gentle manual pressure around the openings of one to five femoral pores, and removing secretion plugs with small forceps. Secretions were placed in small vials, transported on ice, and subsequently stored at -15°C . Protein components of the secretions were isolated by placing whole plugs in methylene chloride for 24 h, then removing the undissolved proteinaceous material and air drying the samples (Alberts, 1990). With stirring in a 100°C water bath, the secretion plugs were subsequently dissolved in 8 Molar (M) urea to a final concentration of $1\mu\text{g}/\mu\text{l}$.

Protein electrophoresis and gel calibration.—Polyacrylamide gel electrophoresis was used to determine the size and relative concentration of protein components (Laemmli, 1970). For each sample, $50\mu\text{l}$ of the protein solution was loaded onto one of three 15% non-reducing sodium dodecyl sulfate (SDS) polyacrylamide gels. Further details of the procedure are presented in Alberts (1990). Following electrophoresis, gels

were stained using a highly sensitive silver staining technique (Switzer et al., 1979). The gels were fixed initially in 50% methanol:10% acetic acid, rinsed with water, and then treated with dithiothreitol before exposure to silver nitrate, a modification that reduces variability in staining and results in more reliable, reproducible staining patterns (Morrissey, 1981). Following impregnation with silver nitrate, the gels were rinsed with water, then developed with continuous agitation in a solution of 15 g sodium carbonate plus $250\mu\text{l}$ 37% formaldehyde in 500 ml water. Once protein bands became evident, development was arrested with 2.3 (M) citric acid monohydrate.

On each of the three gels, a lane of six standards representing proteins of known size (97,400, 66,200, 42,699, 31,000, 21,500, and 14,400 daltons (d); Biorad, Richmond, CA) was run, allowing for calibration of bands across gels. The sizes of all protein bands visible on the gels were determined by comparison, and a presence/absence matrix of species-by-bands was then constructed. One male *D. dorsalis* and one male *I. iguana* were randomly chosen as secretion donors for the interspecific comparison. To examine intraspecific variation in protein composition, two additional matrices were constructed in a similar manner, one for the five samples from *I. iguana* and one for the nine samples from *D. dorsalis*.

Ordination of species and statistical analyses.—To obtain a single score for each species reflecting overall protein band composition relative to other species, an eigenanalysis reciprocal averaging ordination (Ludwig and Reynolds, 1988), similar in theory to a principal components analysis, was conducted on the species-by-bands presence/absence matrix for the 14 iguanid species. Because the data were non-normally distributed and the presence/absence matrix was singular, the reciprocal averaging method (Hill, 1973) was preferred over the principal components technique. The procedure arranges species on the basis of their protein compositions, such that species sharing several bands receive similar ordination scores, while those with dissimilar protein profiles are assigned more divergent scores. A second, analogous ordination was run on the protein band presence/absence matrix for the nine samples of *D. dorsalis*.

Two ordination axes were obtained for each matrix, but only the first was used in subsequent

statistical analyses due to potential problems associated with interpretation of higher order axes (Gauch et al., 1977). To identify the bands that significantly influenced ordination scores, the presence of each band was correlated with the first axis score across species for the interspecific comparison, and across individuals for the gel for *D. dorsalis*, using Spearman rank non-parametric correlations. Bands highly correlated with axis scores contribute strongly to the ordination axis, while uncorrelated bands have little or no influence on axis scores.

With the exception of *Gambelia wislizenii*, each iguanid species was classified according to subfamily as an iguanine (*Brachylophus*, *Iguana*, *Sauromalus*, *Dipsosaurus*) or a sceloporine (*Petrosaurus*, *Uta*, *Urosaurus*, *Sceloporus*, *Phrynosoma*), and according to habitat as arboreal (*Brachylophus*, *Iguana*, *Urosaurus graciosus*, *Sceloporus occidentalis*), terrestrial (*Dipsosaurus*, *Uta*, *Phrynosoma*), or saxicolous (*Sauromalus*, *Petrosaurus*, *Urosaurus microscutatus*, *Sceloporus orcutti*), following Etheridge and de Queiroz (1988). Although *S. occidentalis* could arguably be classified as terrestrial rather than arboreal, this species' habit of perching on wood substrates (Stebbins, 1966) led to the latter classification. The sample of *U. microscutatus* was collected from a population in a rocky habitat, thus it was classified as saxicolous. To determine the relative importance of historical and adaptive influences on variation in secretion composition, the subfamily and habitat classifications were used as factors in a two-way analysis of variance on the first axis ordination scores. A Mann-Whitney test using rank sums was employed to compare the first axis scores of male and female *D. dorsalis*.

Tree construction.—Relationships among femoral gland proteins were also examined with methods designed for phylogeny reconstruction, using computer programs in the PHYLIP inference package (version 3.1, 1988, J. Felsenstein, University of Washington). Each protein component was treated as a separate character, and no *a priori* assumptions about ancestral character states were made, thus the Wagner parsimony method was preferred for tree construction. Because two outgroup species were included in the analysis, the teiid *Cnemidophorus tigris* and the cordylid *Gerrhosaurus major*, the trees could be rooted. One major assumption of tree reconstruction methods is that characters evolve independently (Felsenstein, 1982). Because this criterion is almost certainly violated when protein components of femoral gland

secretions are treated as individual characters, these trees were not expected to necessarily yield the true phylogenetic relationships among species. Rather, tree reconstruction was used as a tool to further examine patterns of similarity in femoral gland proteins across species. Discrepancies potentially indicating convergence in secretion composition were identified by comparing the Wagner trees obtained using femoral gland proteins as characters to an existing tree based on morphological data (de Queiroz, 1987).

RESULTS

Phenetic patterns of similarity.—A summary of band presence in the 16 lizard species studied is presented in Table 1. Because only the size and not the identity of each protein band could be determined from the gels, it is possible that some bands that were scored as common to two species actually represented different protein components of similar size. Without chemical identification of each protein band, it is impossible to determine whether or not two bands that migrate the same distance on a gel represent the same protein. The parsimonious interpretation of the data is that two bands of similar size are the same component, a basic assumption that underlies the analyses reported here.

The mean percentage of protein bands shared among species pairs is 15.2%. When only the 14 iguanid species are considered, excluding *C. tigris* and *G. major*, this figure rises to 17.6%. Among the iguanines and the sceloporines, an average of 39.0% and 25.8% of bands are shared between species, respectively. For four of the lizard genera, *Brachylophus*, *Petrosaurus*, *Urosaurus*, and *Sceloporus*, femoral gland secretions from more than one species were obtained, permitting calculation of the percentage of bands shared between congeners. Although this value ranges from 28.6% in *Sceloporus* to 83.3% in *Brachylophus*, the mean percentage of bands shared between species within a genus, 51.2%, substantially exceeds the mean percentage of bands shared between species in the same subfamily. In the two species for which secretions from multiple males were available, *I. iguana* and *D. dorsalis*, the mean percentage of bands shared rises to 82.5% and 81.7%, respectively.

Ordination of species.—The reciprocal averaging ordination of the 14 iguanid lizard species is presented in Figure 1. The five iguanines re-

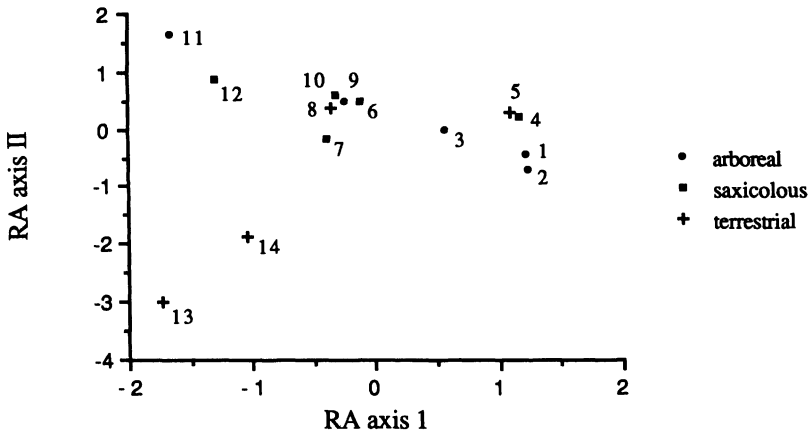


Fig. 1. Results of reciprocal averaging ordination of 14 iguanid lizard species based on femoral gland secretion protein composition. The first ordination axis is plotted on the abscissa and the second ordination axis on the ordinate: *Brachylophus fasciatus* (1), *B. vitiensis* (2), *Iguana iguana* (3), *Sauromalus obesus* (4), *Dipsosaurus dorsalis* (5), *Petrosaurus mearnsi* (6), *P. thalassinus* (7), *Uta stansburiana* (8), *Urosaurus graciosus* (9), *U. microscutatus* (10), *Sceloporus occidentalis* (11), *S. orcutti* (12), *Phrynosoma platyrhinos* (13), *Gambelia wislizenii* (14).

ceived the highest first axis ordination scores, resulting in their placement together at the far end of the first axis. Three of the sceloporine genera, *Urosaurus*, *Uta*, and *Petrosaurus*, had intermediate scores on both axes, and formed a relatively tight cluster. Although the ordination did not group the two species of *Sceloporus* with the other sceloporines, they were placed closer to each other than to any of the other species along the first ordination axis, and they received first axis scores that were closer to the other sceloporines than to the iguanines. The single crotaphytine, *G. wislizenii*, and the sceloporine *P. platyrhinos* received outlying scores on both the first and second axes relative to the other species. *Phrynosoma platyrhinos* was somewhat surprisingly less similar to the other sceloporines than *G. wislizenii*.

Results of the two-way ANOVA on first axis scores confirmed the importance of subfamily membership ($F = 23.84$, $df = 1, 8$, $P = 0.001$) relative to habitat ($F = 0.36$, $df = 2, 8$, $P = 0.71$) in explaining variance in axis scores across species. There was no significant interaction between subfamily and habitat ($F = 0.21$, $df = 2, 8$, $P = 0.81$). Examination of the correlations between band presence and first axis ordination scores revealed significant correlations for nine of the 43 bands examined, indicating that these nine bands (11,500, 13,000, 15,000, 21,000, 23,000, 27,000, 29,000, 40,000, and 41,000 d) contributed strongly to first axis scores. Of these

nine bands, six were found only among the iguanines, providing further support for a first ordination axis separation along subfamilial lines. The single band that showed a significant negative correlation (21,000 d) was present in four non-iguanines, but in only a single iguanine, *I. iguana*.

Patterns of similarity based on phylogenetic reconstruction methods.—Three equally parsimonious trees were obtained using the Wagner parsimony method. The three Wagner trees were very similar, and each separated the sceloporines and the iguanines into two distinct groups. Among the three trees, two slightly different patterns were found for both the sceloporine and the iguanine groups. The pattern observed most often for each subfamily is depicted schematically in Figure 2. Among the sceloporines, *Phrynosoma* and *Sceloporus* were separated from *Urosaurus*, *Uta*, and *Petrosaurus* by the analysis. In accordance with phylogenetic patterns, the two species of *Sceloporus* were grouped together. The pattern in the other branch of the tree was unexpected. *Urosaurus microscutatus* was grouped together with the two species of *Petrosaurus* rather than with its congener, *U. graciosus*. Among the iguanines, *Brachylophus* was separated from *Sauromalus*, *Dipsosaurus*, and *Iguana*. Within this grouping, *Sauromalus* and *Dipsosaurus* were more similar to each other than either was to *Iguana*.

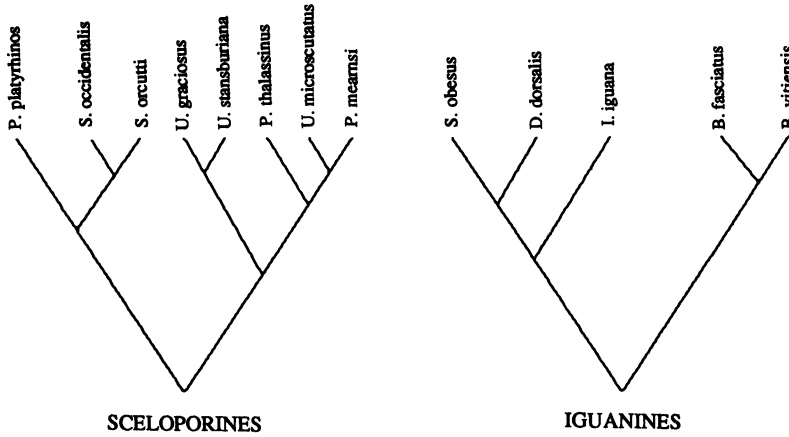


Fig. 2. Branching patterns indicate relationships between proteins in the femoral gland secretions of eight sceloporine and five iguanine lizard species. The trees were constructed using the Wagner parsimony method. Because femoral gland proteins cannot be assumed to be independently evolved characters, the trees are not necessarily indicative of phylogenetic relationships among species. Branch lengths do not reflect degree of similarity.

Intraspecific variation in secretion composition.—Seven of the 13 protein bands identified in the femoral gland secretion samples of *D. dorsalis* were shared by all nine individuals, while six bands showed variation in their presence. All individuals examined differed by at least one protein component, implying the existence of individually distinctive protein profiles in the individuals tested. The percentages of bands shared among individuals are shown in Table 2. Among all nine *D. dorsalis*, the mean percentage of bands shared was 77.4%. When comparisons within sexes were made, however, the mean percent shared rose to 81.7% among the six males and 86.7% among the three females, suggesting that males are more similar to other

males, and females to other females, than individuals of either sex are to individuals of the other.

The reciprocal averaging ordination produced a first ordination axis that separated males from females on the basis of femoral gland secretion composition. All of the females received ordination scores that were clustered at one end of the first axis, and a Mann-Whitney test comparing the scores of females to those of males was statistically significant ($U = 18$, $n_1 = 3$, $n_2 = 6$, $P < 0.05$). For the six bands that varied across individuals, the correlations of band presence with the first axis ordination scores showed that three bands contributed strongly to the ordination scores ($r_s = 0.822$, $r_s = -0.822$, $r_s =$

TABLE 2. PROPORTION OF PROTEIN BANDS SHARED BETWEEN PAIRS OF NINE INDIVIDUAL DESERT IGUANAS.

	Males						Females		
	1	2	3	4	5	6	7	8	9
1	1.0								
2	.818	1.0							
3	.900	.727	1.0						
4	.700	.700	.778	1.0					
5	.800	.800	.889	.875	1.0				
6	.900	.900	.800	.778	.889	1.0			
7	.583	.583	.636	.778	.800	.636	1.0		
8	.727	.727	.800	.778	.889	.800	.800	1.0	
9	.667	.667	.727	.700	.800	.727	.900	.900	1.0

-0.725; $n = 13$, $P < 0.005$ for each). One of these bands was not present in the secretion profiles of any females, but was found in three of the six males, whereas the other two bands were present in the secretions of two and three of the females, respectively, but were absent from the secretions of all males. These results further support the interpretation that the first ordination axis has dichotomized individual *D. dorsalis* on the basis of sex.

DISCUSSION

Comparison of secretion composition across lizard species indicates that much of the variation in femoral gland proteins is accounted for by phylogeny. The ordination of species based on secretion composition produced a first axis that was strongly associated with subfamily, but not with arboreal, saxicolous, or terrestrial habitats. In accordance with their shared phylogenetic history, the iguanines, a monophyletic group exhibiting many unique morphological characters (Etheridge, 1982; de Queiroz, 1987; Etheridge and de Queiroz, 1988), were grouped together at one end of the axis, apart from the other iguanids. Among the sceloporines, three genera, *Urosaurus*, *Uta*, and *Petrosaurus*, were clustered by the ordination. These species all share some derived osteological features, although *Petrosaurus* is most distinct of the three (Etheridge, 1964). Further supporting evidence for the importance of phylogeny is found in the patterns of variation within the genera *Brachylophus* and *Sceloporus*. *Brachylophus fasciatus* and *B. vitiensis*, two closely related species endemic to South Pacific islands (Gibbons, 1981), share a very high percentage of bands, slightly exceeding the percent shared by individuals within *I. iguana* and *D. dorsalis*, and received first axis ordination scores that were virtually identical. The two species of *Sceloporus*, however, share fewer bands than any other genus examined, and received divergent ordination scores. *Sceloporus* contains more species than any other genus in its subfamily and is highly variable osteologically (Etheridge, 1964), indicating that high intrageneric variability in femoral gland secretions is not inconsistent with other phylogenetic patterns within this group.

Several sceloporine species shared more protein bands with *G. wislizenii*, a crotaphytine, than they did with *Phrynosoma platyrhinos*, a sceloporine. In addition to the presence of several distinctive protein bands in the secretions of *P.*

platyrhinos, unextracted secretions in this species are bright orange in color, a feature not exhibited by the other sceloporines examined. Although the genus *Phrynosoma* differs from other sceloporines osteologically (Presch, 1969), it is apparently morphologically closer to the other sceloporines than is *G. wislizenii*, making the observed pattern of variation in femoral gland secretion chemistry unexpected. One possible explanation for discrepancy between the secretions of *P. platyrhinos* and the other sceloporines is its unique diet. The other sceloporines are general insectivores, whereas *P. platyrhinos* feeds almost exclusively on ants (Stebbins, 1966). Evidence for dietary influences on exocrine products exists for other chemical communication systems (Lederer, 1949; Wilson and Bossert, 1963), and it is possible that the unusual diet of this group has influenced the chemistry of its secretions. Unfortunately, the importance of diet cannot be tested rigorously for the set of species examined here because it is almost completely confounded by subfamilial membership. All of the iguanines studied are largely herbivorous, at least as adults (Iverson, 1982), whereas most of the sceloporines are insectivorous (Smith, 1946).

Patterns of similarity indicated by the Wagner trees show that much of the variation in femoral gland protein composition has an historical basis, corroborating the results of the ordination. Although a separation along subfamilial lines was observed, examination of the tree on a finer scale reveals patterns that do not fit phylogenetic expectations. The saxicolous species *Urosaurus microscutatus* is grouped with the two rock-dwelling species of *Petrosaurus*, rather than with its congener, *U. graciosus*. Within this grouping, *U. microscutatus* is closer to *P. mearnsi*, with which it is sympatric, than either species is to *P. thalassinus*. It is possible that similarity between *U. microscutatus* and *P. mearnsi* represents convergence in secretion composition. The surface area of a natural substrate, its porosity, and its chemical charge can strongly influence temporal parameters of pheromone release (Regnier and Goodwin, 1977). Similarity in secretion composition among saxicolous sceloporines may result partially from selection for efficient signal transmission in rocky habitats.

Among the iguanines, *D. dorsalis* and *S. obesus* are grouped together in the Wagner tree, yet morphological data indicate that *Dipsosaurus* is outside the clade formed by most other igua-

nines, including both *Iguana* and *Sauromalus* (de Queiroz, 1987; Etheridge and de Queiroz, 1988). A similar pattern was observed in the ordination, which assigned close scores to *D. dorsalis* and *S. obesus*. One possible explanation for the concordance of *D. dorsalis* and *S. obesus* in secretion chemistry is their similar geographic distribution. Although one species is terrestrial and the other saxicolous, both inhabit desert environments of extreme heat and aridity (Stebbins, 1966). Because the transmission properties of chemical signals, especially volatility and stability, are influenced by environmental factors such as temperature and humidity (Bossert and Wilson, 1963; Regnier and Goodwin, 1977), species that experience similar climatic conditions might be expected to show convergence in their use of secretion components. The similar secretions of *D. dorsalis* and *S. obesus* possibly reflect common adaptation to the desert environment they inhabit. Environmental factors have been implicated previously to explain the low volatility and high thermal stability of femoral gland secretions in *D. dorsalis* (Alberts, 1989a, 1990).

While shared ancestry appears to account for much of the variability in secretion composition at the subfamilial level, it does not fully explain the observed patterns. In addition to the possibility that ecological factors such as diet, climate, and habitat may also explain variation in secretion composition, some of the divergence in secretion composition may be non-adaptive and simply reflect differential rates of evolutionary change in different groups. Although the occupation of arboreal, saxicolous, or terrestrial habitats was not found to explain a significant level of the variation in secretion composition, the observed patterns of similarity among saxicolous sceloporines suggest that a greater number of species belonging to different taxonomic groups should be examined before habitat effects are dismissed.

One implication of interspecific variability in secretion composition is that femoral gland secretions could be used for species discrimination by lizards possessing the ability to differentiate chemical profiles of sympatric species. Intraspecific variation in the secretions of two species, *I. iguana* and *D. dorsalis*, indicates that if chemical differences between individuals are perceived by lizards, then differences in secretion composition conceivably also could be used in conspecific recognition. The possibility that femoral gland secretions function in territorial

marking has been discussed previously (Cole, 1966; Duvall, 1979; Alberts, 1989b). Their high protein content, a feature apparently shared by many species, indicates that they are relatively non-volatile and probably persist for several days after their deposition (Alberts, 1990), a characteristic that is important for effective territorial advertisement. If sexual differences in secretions of *D. dorsalis* are consistent and detectable, then femoral gland secretions may convey sexual identity, although secretions from more individuals need to be examined before a quantitative measure of sexual variation in secretion composition can be made. Field studies have shown that patterns of femoral gland activity differ in male and female *D. dorsalis* (Alberts, 1989b). During the breeding season, all adult males possess active femoral glands, while only unmated females show glandular activity. In males, the secretions probably function in home range advertisement, while in females they may facilitate pairing by allowing unmated females to make their presence known to potential mates. The intraspecific variation documented here suggests that femoral gland secretions potentially transmit useful social information, but further study is required to determine both the extent of intraspecific variation in the secretions of other species, and also the degree to which this variation is perceived and used in communication.

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