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Sources of Intraspecific Variability in the Protein Composition of Lizard Femoral Gland Secretions

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Proteins in the femoral gland secretions of 23 adult and 31 juvenile green iguanas (*Iguana iguana*) were compared using polyacrylamide gel electrophoresis. Similarity coefficients reflecting the degree of band sharing between pairs of individuals were calculated to investigate variability in femoral gland proteins at the individual, familial, and population levels. Although all iguanas examined shared many protein bands, no two individuals possessed identical banding patterns. Similarity coefficients were higher within than between populations, indicating a genetic basis for variation in femoral gland proteins. In juveniles, protein composition was more similar within than between the sexes. Furthermore, among both male and female juveniles, more protein bands were shared within than among clutches. These results suggest that, if differences in protein composition are detected by green iguanas, femoral gland secretions could communicate information useful in conspecific, sex, and kin recognition.

INTRASPECIFIC variation in the composition of chemical signals has been demonstrated in a variety of vertebrates (Wilson, 1970; Albone, 1984). Within a species, variability in chemical signal composition may occur at several levels: between populations, kin groups, sexes, age classes, and individuals within the same kin, sex, and age group (Stoddart, 1980). As hypothesized for invertebrates, intraspecific variation in vertebrate chemical signals probably has both a genetic and an environmental basis (Barrows et al., 1975). In addition to genetic differences, individual variation in diet and bacterial flora may significantly influence the composition of chemical signals (Halpin, 1980; Albone, 1984).

Many lizards possess exocrine glands in the femoral region that are more active in males than in females and undergo an activity cycle coinciding with the breeding season (Cole, 1966; Chiu and Maderson, 1987). Femoral glands are

externally visible as a series of pores through which semisolid plugs are secreted. Secretions from the glands elicit chemosensory investigation in iguanid lizards (Duvall, 1986; Alberts, 1992a) and may function in home range marking (Alberts, 1992b). Several studies indicate androgenic control of femoral gland activity (Maderson and Chiu, 1981; Fergusson et al., 1985; Van Wyk, 1990).

Research on courtship and agonistic displays (Dugan, 1982a; Pratt et al., 1992), nesting and reproductive behavior (Burghardt et al., 1977; Rodda, 1992), and spatial and temporal movement patterns (Bock et al., 1989; Rand et al., 1989) demonstrates that green iguanas, *Iguana iguana*, exhibit a highly developed social system. Although stereotyped headbob displays are used as visual signals in social interactions (Dugan, 1982b), several studies suggest that chemical communication is also an important component of social behavior. Green iguanas possess fem-

oral glands that peak in activity during the mating period (Alberts et al., 1992a). The glands occur in both sexes, although they are larger in males than in females of similar body size (Lazell, 1973; Rodda, 1991). Secretory plugs from the glands contain lipids (Weldon et al., 1990) and proteins (Alberts, 1991). In males, the lipid concentration of the secretions increases during the breeding season, and a greater degree of unsaturation occurs in the carbon chains of free and esterified fatty acids. It is possible that these features render secretions more detectable at this time of year due to increased volatility (Alberts et al., 1992b). Behavioral and endocrinological studies suggest that femoral gland secretions may be important in establishing and maintaining dominance relationships among males, particularly during the mating period (Alberts et al., 1992a).

Assessing the adaptive significance of variability in chemical signal composition requires chemical studies on structural variation as well as behavioral studies on the extent to which this variation is perceived and utilized in social behavior. Documentation of how chemical variation is partitioned within a species can be useful in predicting the range of information potentially communicated by chemical signals. In this study, we examine variability in the protein components of femoral gland secretions of male and female green iguanas at the individual, familial, and population levels. The possible implications of intraspecific variation in secretion chemistry for social communication are discussed.

METHODS

Study animals and sample collections.—Femoral gland secretions were obtained from two populations of green iguanas. Secretions from 15 captive adult males were collected at the Iguana Management Project in Orotina, Costa Rica, in Nov. 1989. These males hatched from eggs laid by free-ranging females in the vicinity of National Park Soberania, Panama. Secretions also were obtained from eight adult male, 20 hatchling male, and 11 hatchling female captive green iguanas at the San Diego Zoo once per month from Nov. 1989 through Sept. 1990. These animals came from artificially incubated eggs collected from free-ranging females in a population near Democracia, Belize. The source of each egg was known; thus these hatchlings could be assigned to one of six clutches. Because paternity was unknown, genetic relatedness among hatchlings within clutches potentially varied from half to full siblings. The animals at the

San Diego Zoo were all fed a similar diet, consisting of fresh greens supplemented with a commercially available cereal product (Hill's product #6920).

Samples were collected by applying gentle manual pressure around the openings of the two most proximal femoral pores on each leg and removing secretion plugs with small forceps. Secretion plugs were placed immediately in CH_2Cl_2 for 24 h, and proteins were subsequently isolated by removing the undissolved proteinaceous material (Alberts, 1991). After isolation, proteins were dissolved to $1 \mu\text{g}/\mu\text{l}$ in a nonreducing disruption buffer containing 2% SDS, 8 M urea, 62.5 mM Tris-HCl (pH 6.8), 10% glycerol, and 0.0025% bromphenol blue and stored at -80°C .

Electrophoresis and staining procedure.—The relative molecular weights of protein components present in the femoral gland secretions of individual green iguanas were estimated using polyacrylamide gel electrophoresis (Laemmli, 1970). After heating for 5 min in a boiling water bath, $10 \mu\text{l}$ of protein solution from each sample were loaded onto 15% nonreducing polyacrylamide gels. Gels were run at 13 mA until the bromphenol blue tracking dye exited the stacking gel, then at a constant 16 mA until the dye front reached the end of the gel.

Following electrophoresis, gels were fixed in 50% methanol : 10% acetic acid for 30 min. Gels were stained by initially treating them with 0.5% dithiothreitol for 30 min (Morrissey, 1981), then exposing them to 0.1% silver nitrate (Switzer et al., 1979) for 30 min. Gels were rinsed with water and subsequently developed with continuous agitation in a solution of 15 g sodium carbonate, $250 \mu\text{l}$ 37% formaldehyde, and 500 ml water until protein bands became evident. Development was halted by the addition of 2.3 M citric acid.

Gel calibration.—A lane of six low molecular weight standards (14,000, 21,500, 31,000, 42,699, 66,200, 97,400 daltons; Biorad, Richmond, California) was run on each gel to permit calibration of bands across gels. The size of each protein was determined by comparison. Because only the size, and not the identity, of each protein could be determined from the gels, it is possible that some bands scored as common to two individuals were actually different proteins of similar molecular weight. Without a detailed characterization of each protein band, it is impossible to determine whether two bands that migrate to the same position on a gel are the same protein. The parsimonious interpre-

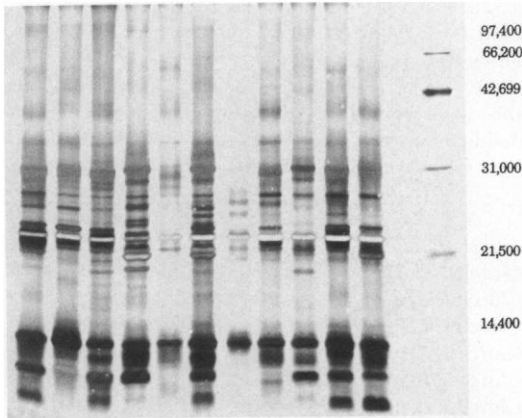


Fig. 1. Representative SDS polyacrylamide electrophoresis gel showing banding patterns of femoral gland proteins from 11 adult male green iguanas. Molecular weight standards are on the right.

tation of the data is that two bands of similar size in these secretions are the same component, an assumption that underlies the analyses reported here.

Similarity coefficients, reflecting the degree of band sharing between pairs of individuals (Lynch, 1990), were calculated according to the formula:

$$S_{AB} = \frac{2(AB)}{A + B}$$

where A equals the total number of bands in individual A's profile, B equals the total number of bands in individual B's profile, and AB equals the total number of protein bands shared by individuals A and B. This index varies from 0, when no bands are shared in common, to 1, when banding patterns are identical.

Statistical analyses.—Single and two-factor analyses of variance were employed to test for differences in the mean similarity coefficient between pairs of male iguanas from Belize and Panama source populations, pairs of male and female hatchlings, and pairs of hatchlings belonging to different clutches. Multiple comparisons were made using Fisher's protected least significant difference test (Carmer and Swanson, 1973).

RESULTS

Although all of the iguanas surveyed shared many protein bands, certain proteins were absent in some individuals, and no two individuals possessed identical banding patterns (Fig. 1). In

TABLE 1. MEAN SIMILARITY COEFFICIENTS FOR FEMORAL GLAND PROTEINS OF 23 ADULT MALE GREEN IGUANAS BELONGING TO POPULATIONS IN BELIZE AND PANAMA. The number of pairs of individuals examined to obtain each coefficient is given in parentheses. Standard errors are given.

Comparison	Similarity coefficient
Belize population (28)	0.773 ± 0.014
Panama population (105)	0.761 ± 0.009
Between populations (120)	0.435 ± 0.006

particular, there were bands at 19,000 and 39,000 daltons that appeared to be very intense in some individuals but entirely absent in others. The bands below 14,000 daltons also showed a notably high degree of variation in both their presence and intensity across individuals. Monthly samples were collected over a one-year period from the iguanas housed at the San Diego Zoo, permitting examination of seasonal variation in secretion composition. For the 39 individuals surveyed, secretion samples collected from the same individual in different months produced identical banding patterns, indicating that protein composition is constant over time.

Interpopulational comparisons of the banding patterns of unrelated adult males demonstrated geographic variation in femoral gland protein composition (Table 1). Males belonging to the same source population shared more protein bands in common than those belonging to different source populations ($F = 536.76$, $df = 2$, 250 , $P = 0.0001$). Fisher's protected least significant difference test (critical PLSD = 0.03) revealed that a greater proportion of bands were shared within both the Belize (PLSD = 0.35, $P < 0.05$) and Panama (PLSD = 0.34, $P < 0.05$) populations than between the two populations. Within each of the two populations, the degree of similarity in protein composition between males was not significantly different (PLSD = 0.01, $P > 0.05$).

For the animals housed at the San Diego Zoo, comparisons of femoral gland proteins indicated both sexual and familial components of variation (Table 2). Two-factor analysis of variance showed that femoral gland proteins were more similar within than between the sexes ($F = 4.46$, $df = 2$, 459 , $P = 0.01$) and also among siblings than among nonsiblings ($F = 17.66$, $df = 1$, 459 , $P = 0.0001$). The highest mean similarity coefficients were evident among siblings of the same sex, whereas siblings of the opposite sex tended to share an intermediate proportion of protein bands. For within and between sex compar-

TABLE 2. MEAN SIMILARITY COEFFICIENTS FOR FEMORAL GLAND PROTEINS OF 20 MALE AND 11 FEMALE GREEN IGUANAS FROM THE SAME AND DIFFERENT CLUTCHES. The number of pairs of individuals examined to obtain each coefficient is given in parentheses. Standard errors are given.

Comparison	Similarity coefficient
Among males	
siblings (30)	0.840 ± 0.021
nonsiblings (160)	0.744 ± 0.007
Among females	
siblings (8)	0.835 ± 0.039
nonsiblings (47)	0.745 ± 0.006
Between the sexes	
siblings (28)	0.771 ± 0.017
nonsiblings (192)	0.745 ± 0.007

sons, the lowest similarity coefficients were found among nonsiblings.

Further support for an underlying genetic basis for variation in protein composition was obtained by comparing band sharing within and between clutches. For each of the six clutches examined, the mean similarity coefficient for pairs of individuals within a clutch exceeded that between clutches (Table 3). Statistical comparisons among clutches were not attempted due to the small number of pairings possible for some clutches.

DISCUSSION

Green iguanas exhibit individual differences in the protein composition of their femoral gland secretions that are constant over time. These results differ from those for femoral gland lipids, which exhibit significant seasonal variation but little individual variation (Alberts et al., 1992b). If differences in protein composition are detected by green iguanas, femoral gland secretions could function in the discrimination of individual conspecifics. Behavioral experiments indicate that adult male green iguanas respond to femoral gland secretions of unfamiliar conspecific males with significantly higher rates of chemical investigation than they do to their own secretions or those of familiar males (Alberts and Werner, in press). The protein fraction of the secretions elicits higher rates of tongue flicking than does the lipid fraction, but a greater proportion of tongue flicks are directed toward the air in the presence of the lipids alone. It is possible that femoral gland

TABLE 3. MEAN SIMILARITY COEFFICIENTS FOR FEMORAL GLAND PROTEINS OF 31 GREEN IGUANA HATCHLINGS BELONGING TO SIX DIFFERENT CLUTCHES. The mean similarity coefficient among all hatchlings is shown for comparison. The number of pairs of individuals examined to obtain each coefficient is given in parentheses. Standard errors are given.

Comparison	Similarity coefficient
Clutch A (15)	0.832 ± 0.031
Clutch B (3)	0.945 ± 0.016
Clutch C (3)	0.938 ± 0.017
Clutch D (10)	0.785 ± 0.026
Clutch E (6)	0.796 ± 0.051
Clutch F (28)	0.786 ± 0.018
Between clutches (400)	0.748 ± 0.005

lipids permit initial detection of secretion deposits in the environment through the chemoreception of volatiles, whereas low volatility proteins provide more detailed information regarding the identity of the signaller after secretion deposits are localized. Proteins can be detected by the vomeronasal system (Wysocki et al., 1985; Halpern, 1987) and may function as chemical signals in other vertebrate chemical communication systems (Goodrich and Mykutowycz, 1972; Singer et al., 1984; Belcher et al., 1990). Because they have well-developed olfactory and vomeronasal systems, green iguanas are probably capable of perceiving a wide range of chemical stimuli (Gabe and Saint Girons, 1976; Burghardt et al., 1986).

Among green iguanas, genetic differences between populations that may be related to restricted movement patterns and nest site distribution have been demonstrated (Bock and McCracken, 1988). Differences in femoral gland proteins among green iguanas belonging to different populations are not unexpected given that much of the variation in these proteins among different lizard species has been shown to have a phylogenetic basis (Alberts, 1991). In general, closely related species have femoral gland secretions that are chemically more similar than more distantly related species. These results suggest that the protein composition of femoral gland secretions diverges in isolated lizard populations over time. Differences in femoral gland secretion chemistry may partially contribute to reproductive isolation during speciation, but this possibility remains hypothetical without comprehensive chemical analyses of secretions across species and supporting behavioral data on their social functions.

In this study, green iguanas belonging to dif-

ferent populations shared nearly half of their protein components, a substantially higher fraction than that shared among different species within the Iguanidae (17.6% based on a comparison of 14 species; Alberts, 1991). Components that are shared among different populations may provide the basis for species recognition in green iguanas. The distinctive protein profiles of individual green iguanas may result either from further genetic differences between individuals within populations or from physiological, dietary, or environmental influences (Halpin, 1980). Because clutch membership was found to explain a significant proportion of the variance in band sharing across individuals, genetic influences on femoral gland secretion chemistry are important not only between populations, but also within them. Variance in protein composition not explained by population, sex, and clutch differences could provide the basis for recognition of individual conspecifics.

The finding that femoral gland proteins were more similar among clutchmates than among nonclutchmates provides a potential kin recognition mechanism. This may partially explain why hatchling green iguanas associate preferentially with kin even when they have been raised apart (Werner et al., 1987). Hatchlings have been observed to lick each other frequently when dispersing from communal nests (Burghardt et al., 1977), suggesting that chemical signals may partially mediate aggregation in young iguanas. Behavioral tests comparing the responses of hatchling green iguanas to the secretions of siblings and nonsiblings are necessary to evaluate whether femoral gland secretions transmit information regarding kinship.

Kin recognition based on femoral gland secretions, if it occurs, may cease to operate in females relatively early in development. The rate of secretion production in male and female hatchlings is similar until approximately one year of age, but thereafter, secretion production only continues to increase in males (Alberts et al., 1992a). Once female green iguanas attain sexual maturity, femoral gland activity is negligible (Rodda, 1991). The physiological mechanism responsible for diminished secretion production in females may be an increase in circulating estrogens, a factor which inhibits activity of these glands in other lizards (Chiu et al., 1975).

Sexual dimorphism in femoral gland proteins suggests that these secretions potentially communicate information useful in sex recognition prior to the time femoral gland activity in females begins to diminish. Because males partic-

ipate in dominance interactions almost immediately posthatching (Phillips et al., 1993), it may be especially important for them to be able to recognize and react appropriately toward particular conspecifics. Under these circumstances, the ability to distinguish male from female hatchlings could be advantageous in avoiding unnecessary aggressive encounters. Approximately one year posthatching, coinciding with the reduction in female femoral gland activity, juvenile male and female green iguanas begin to diverge in several other morphological and behavioral traits. Behavioral testing at different stages of ontogeny would be useful in assessing the degree to which sex recognition among hatchlings and juveniles, if it occurs, may depend on chemical cues, visual cues, or a combination of signals in both sensory modalities.

This study documents differences in femoral gland proteins between populations, kin groups, sexes, and individuals within the same sex and kin group. The existence of this variation is a minimum requirement if these secretions are to function effectively in conspecific recognition (Beecher, 1989), but its occurrence alone does not address whether these chemical differences are detectable to green iguanas. Even if variation in femoral gland composition is perceived by green iguanas, individuals are only expected to respond differentially toward conspecifics when it is beneficial for them to do so (Walls, 1991). Without experimental testing to ascertain that intraspecific variation in femoral gland proteins is detected and a clear demonstration of its utility in social behavior, hypotheses concerning the adaptive significance of differences in femoral gland secretion chemistry remain speculative.

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New Species of Cardinalfish, *Archamia goni* (Pisces: Apogonidae), from Taiwan

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Archamia goni, a new species of cardinalfish is described from 24 specimens collected from western and southwestern Taiwan. It is distinctive in having a transparent body, no obvious color markings, usually 15–16 anal rays, three hypurals, a more elongate body depth 2.7–2.9 standard length, first dorsal spine long (more than three-quarters of the second dorsal spine), and a tiny basi-caudal spot (less than a quarter of caudal peduncle). A key to all species of this genus is also presented.

ARCHAMIA is distinguished from other genera of the family Apogonidae, by a very compressed body, 12–18 anal-fin rays and a distinctive neurocranium (Fraser, 1972). Lachner (1951) reviewed this genus which includes six species. *Archamia biguttata* and *A. dispilus* are new. *Archamia leai* Waite (1916), not included in his paper, should be considered valid. Lachner and Taylor (1960) and Smith (1961) described *A. melasma* and *A. mozambiquensis* from Australia and Mozambique Island, respectively. The total number of valid species of the genus *Archamia* is nine.

In Taiwan, five species were reported previously (Shao and Chen, 1986). They were *A. buruensis*, *A. dispilus*, *A. biguttata*, *A. fucata*, and *A. lineolata*. During recent reexamination of all specimens of cardinalfishes from Taiwan, we found that some specimens previously identified

as *A. lineolata* in Shen and Lam (1977) and Shao and Chen (1986) represented a new species. These specimens differ from other *Archamia* in that they have a transparent body and possess a tiny basi-caudal spot; their anal-fin ray counts, hypural type, body depth, and first dorsal spine length also differ.

MATERIALS AND METHODS

The specimens were collected by diving, bottom trawling, or impingement of intake waters of power plants. Some fish were photographed prior to preservation. All specimens have been deposited in the following institutions: Museum of the Institute of Zoology, Academia Sinica (ASIZP); Bernice Pauahi Bishop Museum, Honolulu (BPBM); Northern Territory Museum, Darwin (NTM); the Museum of the Department