Individual, Sexual, Seasonal, and Temporal Variation in the Amount of Sagebrush Lizard Scent Marks

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Abstract Although many animals deposit scent marks, previous studies have focused almost entirely on rodents or on the chemical structure of the signal. Here, we study the quantity and temporal pattern of chemical deposition by the territorial sagebrush lizard *Sceloporus graciosus*, measuring both femoral pore and fecal deposits. Specifically, we tested whether variation in deposition is a good cue of individual and sexual identity and/or whether it is more closely associated with body size and reproductive state, indicators of physiological condition. The results support the latter hypothesis. We found that although the amount of fluid deposited on a single perch (rarely quantified in mammals) carries little information on individual or sexual identity, it reflects the physiological condition and reproductive state of individual lizards and is replenished on a roughly weekly cycle, potentially providing additional information on the producer's activity level. The amount of deposition may thus provide important information to chemical receivers making mate choice and territorial defense decisions. The results further suggest that seasonal increases in gland production allow lizards to mark more sites rather than to influence the quality of the signal on a single perch.

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Introduction

In many animals, the behavior of scent marking, including spatial and temporal patterns of deposition, can supplement a chemical signal with information about the producer's activity, physiology, or motivational state. Many animals leave chemical signatures passively wherever they go, offering a receiver information about their general activity (see review by Wyatt, 2003). Others modify the quantity and quality of chemical signals by changing their position with respect to the wind, by wing fanning, or by urinating, defecating, or rubbing against a substrate. For example, voles scent-mark in response to chemical signals left by other animals (Wolff et al., 2002; Mech et al., 2003). In rodents, there are considerable individual and seasonal differences in the frequency of scent marking (Nevison et al., 2003; Ferkin et al., 2004), such that the deposition of chemical signals also contains information on the producer's individual identity and reproductive state. Despite major recent advances in determining the structural composition and functional use of chemical signals, little is known about the quantity and temporal pattern of chemical deposits in nonrodent taxa (Wyatt, 2003). In this study, we document patterns of sexual, seasonal, and individual variation in chemical deposition by *Sceloporus graciosus*, the sagebrush lizard, and test hypotheses to determine whether the quantity of deposits carries information on the individual and sexual identity of resident animals, or whether it better reflects physiological condition.

The chemical structures of lizard secretions convey information on the individual, sex, population, and species identity of producing animals (Alberts et al., 1993; Escobar et al., 2001). As reviewed by Mason (1992) and Halpern (1992), most lizards produce chemical secretions in skin or specialized glands and have highly developed chemical discrimination abilities. Many species can use olfaction to distinguish the sex (Labra and Niemeyer, 1999; López and Martín, 2001), social status (Alberts et al., 1994; Molina-Borja et al., 1998), and body size (Aragón et al., 2000) of conspecifics. They also can use chemical cues to identify preferred prey (Cooper and Habegger, 2000) and to avoid predation (Downes, 2002). An impressive diversity of lizard species can distinguish familiar from unfamiliar conspecifics on the basis of chemical cues (Aragón et al., 2001, 2003; Labra et al., 2001; Bull and Lindle, 2002).

The quantity of chemical produced by individual lizards also exhibits intraspecific variation and may be used to transfer information on physiological or reproductive condition as well as identity. As reviewed by Mason (1992), chemical-secreting glands are usually larger and more active in breeding males than in females or juvenile animals. For example, male green iguanas, *Iguana iguana*, maximize production of femoral pore secretions during breeding months, and pore size is associated with plasma levels of testosterone and visual display behavior (Alberts et al., 1992). Testosterone implants cause female whiptail lizards (*Cnemidophorus uniparens*) to exhibit the large, active femoral pores typical of males (Wennstrom and Crews, 1998; Crews et al., 2004), and juvenile tree lizards (*Urosaurus ornatus*) treated with testosterone develop larger femoral pores (Hews et al., 1994).

In contrast, the deposition of lizard chemical signals has received minimal study, making it difficult to determine whether the frequency of scent marking is an

important element of the chemical signal that may also evolve via natural and sexual selection. Here, we monitored lizard scent marks on a primary perch for 35 consecutive days before and 21 d after a hibernation period. We then used these data to determine whether the amount of secretion is better explained by individual and sexual differences, and/or whether they are better explained by general physiological (as reflected by body size and time in captivity) and reproductive condition (as reflected by season). Because these hypotheses are not mutually exclusive, we used multiple regression analyses to compare the relative importance of each factor. We further tested for the importance of individual as opposed to physiological differences by comparing the amount of secretion produced by the same lizards in different seasons. Finally, we examined the time series of chemical deposition to determine how often scent marks were replenished. Although we focused on femoral pore secretion deposits, we also measured fecal spots, which may also carry chemical information (see Mason, 1992).

Methods and Materials

Animals and Housing

Sagebrush lizards are small, insectivorous lizards found throughout the western US. In the field, both males and females are active from mid-March to September. Males are especially territorial in May and June (during the mating season), whereas both sexes defend territories aggressively from July through September (Martins, 1991, 1993). We used 82 males and 49 females that were captured near Wrightwood in southern California (34°23′30″N, 117°42′W) in two separate collections (May 2002 and 2003) and established in separate rooms of our laboratory colony at Indiana University. We used only adult animals. Males were slightly larger than females in both snout-to-vent-length [SVL; male = 5.8 ± 0.04 cm (mean ± SE); female = 5.7 ± 0.04 cm] and weight (male = 8.8 ± 0.17 g; female = 8.1 ± 0.14 g).

Lizards were kept under standard housing, lighting, feeding, and hibernation conditions. For most of the year, individuals were housed in 5-gal aquaria, visually isolated from their immediate neighbors by opaque cardboard barriers, but able to see animals on other cage racks across the room (2–3 m away). Each aquarium was equipped with sand substrate, a water dish, and a split-level brick perch (5.5 cm wide × 21.5 cm long × 6.5/11 cm tall). Each row of cages was illuminated on a 12-hr light cycle by two fluorescent light bulbs stretched across the row and by a single 40-W incandescent bulb hung directly over the highest level of the brick perch on one side of each cage. Although air temperature outside the cages was held at a constant 28°C, the brick perch warmed to as much as 4°C higher than other parts of the cage and was used frequently by active animals. Lizards were watered and misted daily and were fed three times each week with *ad lib* mealworms and vitamin-enriched crickets. Once every 2 wk, large fecal material was removed. From June to September, animals were placed in groups of two to eight animals in 3 × 3 m outdoor enclosures (prior to experiments). In November–January, animals were allowed to hibernate in individual cloth bags at 11°C (during the experimental period; see next section).

One room housed animals (35 males and 24 females) that had been in captivity for more than 1 yr, having been captured in May 2002 and undergoing one period in the outdoor enclosures and one hibernation period before entering the experiment in

2003. The second room housed animals that were brought into the lab in May 2003 but did not spend time in the outdoor enclosures or undergo hibernation before beginning the experiment. Lizards increase in SVL continuously as adults, such that body size and weight are reasonable indicators of physiological condition. Lizards grew quickly in the outdoor enclosures, such that animals that had been in captivity for longer were also slightly larger (SVL = 5.8 ± 0.04 cm compared to SVL = 5.7 ± 0.04 cm).

Chemical Sampling

Although lizards move and potentially deposit secretions throughout their cages, we measured only secretions deposited on the split-level brick, a preferred basking perch. In the field, *Sceloporus* lizards defend several preferred basking perches, leaving the intervening space undefended such that there is considerable home range overlap between individuals (Sheldahl and Martins, 2000). We limited the current study to deposits on a single preferred perch to ensure that our efforts addressed territorial use of chemical deposits rather than general activity. We used white marking tape to attach white paper towels to the top surface of the single brick in each cage. We changed the paper towels daily so that spots could be counted and measured. Used towels were placed under a black light, which makes the femoral pore secretion spots (FPSs; which are UV-reflective, Alberts, 1993) visible to a human observer. Fecal spots are not UV-reflective, and hence were easily distinguished from femoral pore spots. We counted and measured the diameter (to the nearest 0.5 mm) of each femoral pore and fecal spot, using the radii (r) to estimate total area of spots for each lizard on each day (area = $\sum \pi r^2$, where the sum is across all femoral pore or fecal spots produced by one lizard in 1 d).

Data were collected daily from 13 October to 16 November 2003 (35-d prehibernation sequence) and then again from 26 January to 15 February 2004 (21-d posthibernation sequence). During the intervening period, animals were measured, weighed, and allowed to hibernate. Data were not collected 1 wk before and 1 wk after hibernation. In captivity, sagebrush lizards will remain active for 10 or more months of the year, with females readily laying two successive clutches of eggs. The prehibernation period of our study corresponds with a period of territorial aggression in which animals of both sexes actively exclude conspecifics of both sexes from their preferred feeding and basking sites. In contrast, the posthibernation period corresponds to the early mating season when both males and females were at peak activity. During the mating season, males extend their territories into larger areas, each of which encompasses the smaller home ranges of several females, whereas females reduce aggressive territorial behavior. Territorial aggression is stronger in males than in females, and this sexual difference is more pronounced during the mating season than afterwards (Martins, 1993). Thus, if femoral pore or fecal spots are used in territorial defense, we also might expect them to be larger or more abundant in males than in females, especially during the mating season.

Statistical Analyses

We began by using generalized linear mixed models [GLMMs, implemented using the GLIMMIX procedure of SAS (2005)] to estimate the relative importance of identity (individual and sex) and condition (season, body size, and time in captivity) in explaining variation in femoral pore spot deposition. GLMMs are regression-type

models that rely on a family of exponential distributions instead of the usual normal distribution to describe the response variable (in our case, spot number or size). The SAS GLMMIX procedure chooses from among discrete (e.g., Poisson, negative binomial) and continuous (e.g., normal, gamma) exponential distributions using likelihood statistics to find the best fit to the data.

We fitted two GLMMs (one model for spot number and a second model for spot area) to describe the effects of various factors on variation in femoral pore spot deposition. The factors included individual identity (codes for 128 animals), sex (male or female), body size (SVL and weight in grams, as measured just before hibernation), and time in captivity (0 or 1 to distinguish the two collection periods corresponding to 5 or 17 mo in captivity) as potentially relevant predictors. We also included a factor for fecal deposition (fecal spot number and area) for comparison. We report results from analyses using type III sums of squares, which estimate effects for each factor while taking all other variables into account. Residual analyses confirmed that we did not violate the homoscedasticity assumptions of these models.

As a second test of the same hypothesis, we estimated Pearson product moment correlations between daily averages of spot number and area, calculated for each lizard before and after hibernation. Strong correlations indicate the importance of individual identity in determining deposition quantity. Although the counts and areas were not normally distributed, average spot number for a single lizard across several days was close to normal. For comparison, we did the same calculations for both femoral pore and fecal spots and estimated also correlations between femoral pore and fecal spots.

Finally, we examined the temporal pattern of spot deposition. First, we assumed that lizards were temporally synchronized, averaging spot number across all lizards on each day of our sample. This is a reasonable expectation because all animals were kept on identical environmental, husbandry, and feeding regimes for at least 5 mo prior to and during data collection. Again, although the counts are not normally distributed, the averages across all of our lizards on a single day were well simulated by a normal distribution. We used these averages to fit time series models, forecasting across a single series of 56 d (35 d before hibernation + 21 d afterwards) to maximize our predictive ability.

Results

Although all lizards produced FPS on at least 1 d in the 35-d sequence before hibernation, 10 of 82 males and 5 of 49 females did not contribute to the 21-d posthibernation data set. The number of FPS deposited onto the paper towels ranged between 0 and 11 per day (Fig. 1A). Most lizards deposited spots on the brick perch on fewer than 30% of the days in our study. Femoral pore spots varied considerably in size, with most spots being less than 3 mm^2 in area, but a few ranging as high as 18 mm^2 (Fig. 1B). Distributions of fecal spot numbers were similar, but less dispersed, with fewer lizards exhibiting the rare large numbers of spots observed for femoral pore secretions (Fig. 1A). Fecal spots were sometimes larger, ranging up to 40 mm^2 in area (Fig. 1B).

The number and area of femoral pore spots were explained better by physiological condition than by individual identity or sex. Counts of femoral pore
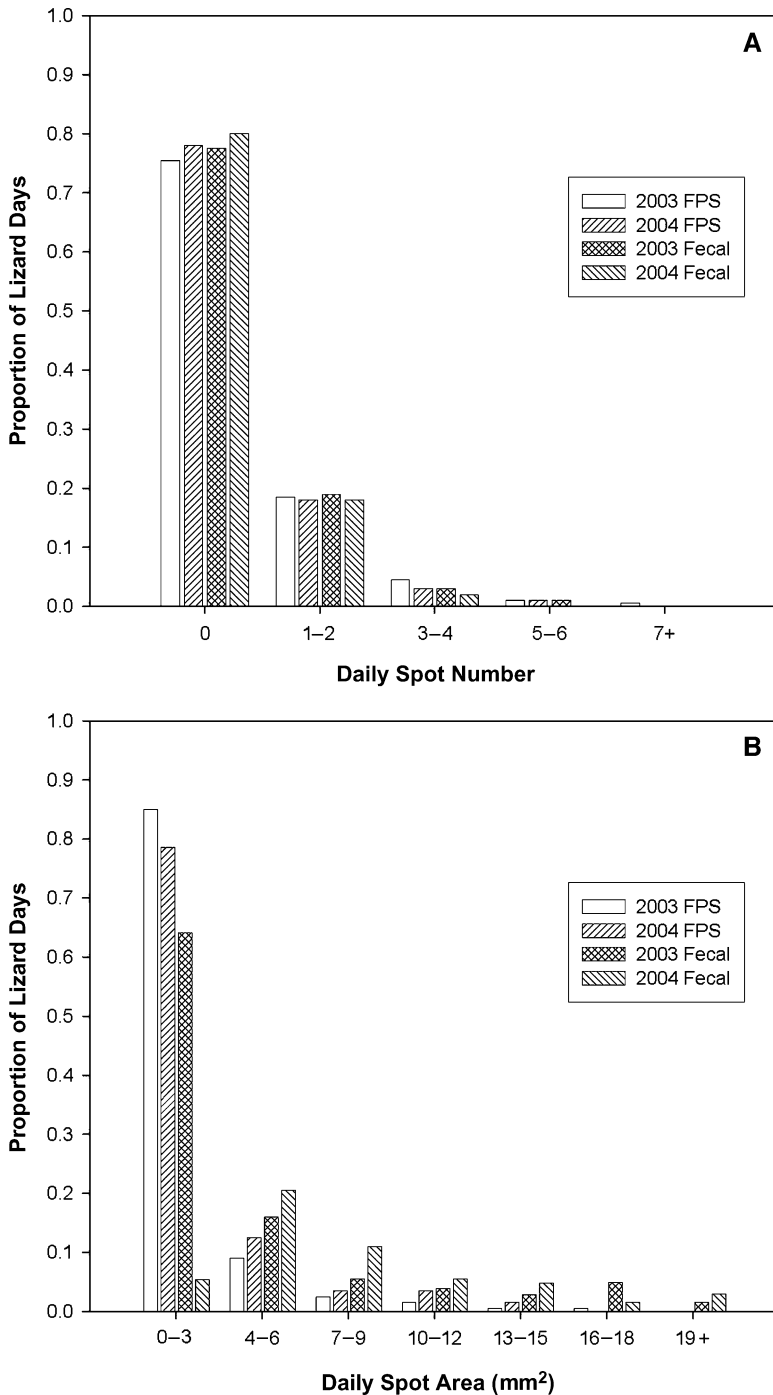
Fig. 1 Distribution of the number (A) and size (B, area in mm^2) of spots produced each day, combining data from both sexes and across the full 56 d of our experiment. 2003: Prehibernation, territorial season. 2004: Posthibernation, mating season

Table 1 *F* Values and predicted effect size estimated by general linear mixed models of femoral pore secretion spot (FPS) number and size (area in mm^2)

Factor	Number[a]	Predicted effect (%)	FPS size[b]	Predicted effect
Season[c]	16.18*	−20	16.24*	0.16
Sex[c]	0.43	−2	2.00	0.08
Captivity[c]	10.41*	−23	111.15*	0.54
Length (mm)	7.19*	−33	0.40	−0.15
Weight (g)	2.37	7	0.52	0.03
Fecal spot no.	15.75*	14	1.91	0.04
Fecal spot area	5.89	1	0.06	0.00

[a] $df = 6993$, distribution = negative binomial, link function = log.

[b] $df = 1643$, distribution = lognormal, link function = identity.

[c] Prehibernation territorial season = 0, mating season = 1; males = 0, females = 1; 17 mo in captivity = 0, 5 mo in captivity = 1.

*$P < 0.01$.

spots were too widely dispersed to be described well by normal or Poisson distributions, but a GLMM with a negative binomial distribution and a log-link function provided a good fit to spot counts. Femoral pore spot area was described better by a lognormal distribution. There was a seasonal effect on both FPS number and area (Table 1). Lizards deposited about 20% fewer FPS during the mating season than during the prehibernation territorial season and increased FPS area by about 0.16 mm^2. Moreover, lizards with longer snout-vent lengths produced fewer, but not smaller, spots (Table 1). Although weight was not a good predictor of either response variable, time in captivity appeared as a related and highly significant predictor, with animals that had spent more than a year in captivity producing fewer but larger FPS than did animals that had been in captivity for only 5 mo. Lizards that had been in captivity for more than 1 yr were also slightly larger ($F = 4.1$, $df = 1,121$, $P < 0.05$ for SVL, including sex also in the model) and considerably heavier ($F = 13.6$, $df = 1,121$, $P < 0.001$) than animals that had been in the lab for a shorter

Table 2 Pearson product-moment correlations between number and size (mm^2) of spots in the same (repeatability) and different years

|	FPS size	Fecal no.	Fecal size
2003 (prehibernation territorial period)			
FPS no.	0.30*	0.18**	−0.14
FPS area		0.26*	0.44*
Fecal no.			0.41*
2004 (mating season)			
FPS no.	0.63*	0.58*	0.36*
FPS area		0.34*	0.45*
Fecal no.			0.53*
Repeatability (2003 to 2004)			
FPS no.	0.08		
FPS area	0.16		
Fecal no.	0.08		
Fecal area	0.39*		

*$P < 0.01$.

**$P < 0.05$.

period. In using type III SS to estimate GLMM parameters (Table 2), we confirmed that time in captivity was an important factor even after differences in body size had been taken into account. Surprisingly, sexual differences were small and did not contribute to variation in FPS number or area, despite visibly larger femoral pores in males, especially during the mating season. Animals that produced more fecal spots also produced more FPS, but size of fecal spots was not related to FPS number or size.

In our second test, individual lizards that produced more or larger spots during the territorial season did not tend to be the same animals that produced more or

Fig. 2 (A) Relationship between number of femoral pore secretion spots (FPS) in territorial and mating seasons ($r = 0.08$, $P > 0.05$). Size of FPS and number of fecal spots give very similar patterns (Table 2). (B) Relationship between size of fecal spots in the two seasons is statistically significant ($r = 0.4$, $P < 0.05$), but probably because of a single influential outlier (Table 2)
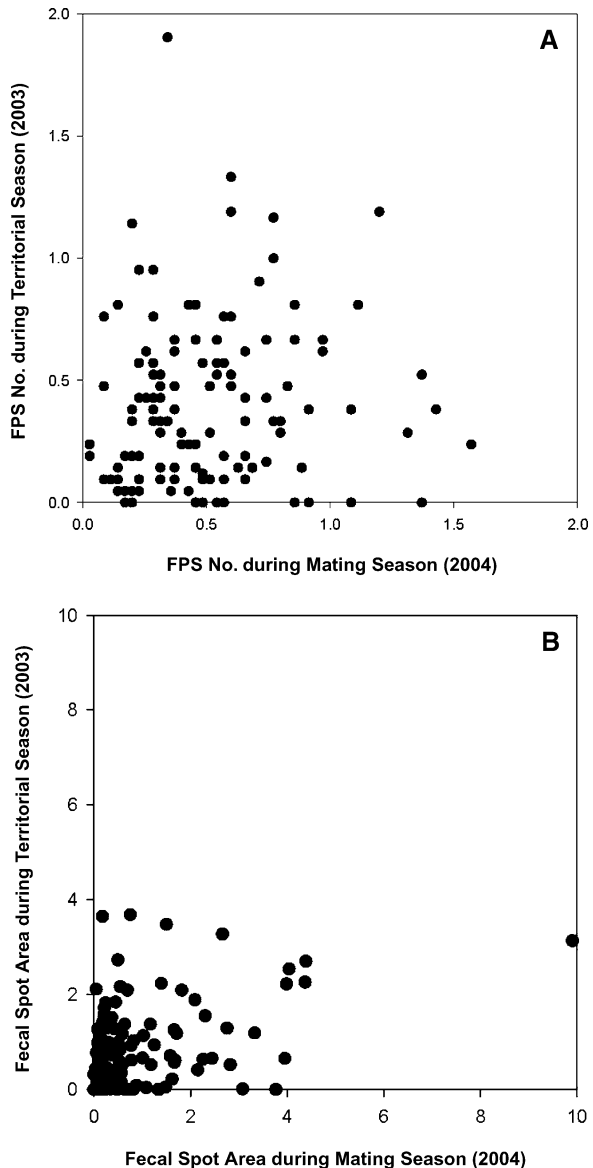
larger spots during the mating season (Table 2, Fig. 2A). Only the area of fecal spots showed a positive relationship between seasons, and this relationship seems to be driven by outliers (Fig. 2B). For the most part, measures of femoral pore and fecal spot deposition were positively associated with each other within but not across seasons (Table 2). The number of FPS was only loosely associated with fecal spots during the
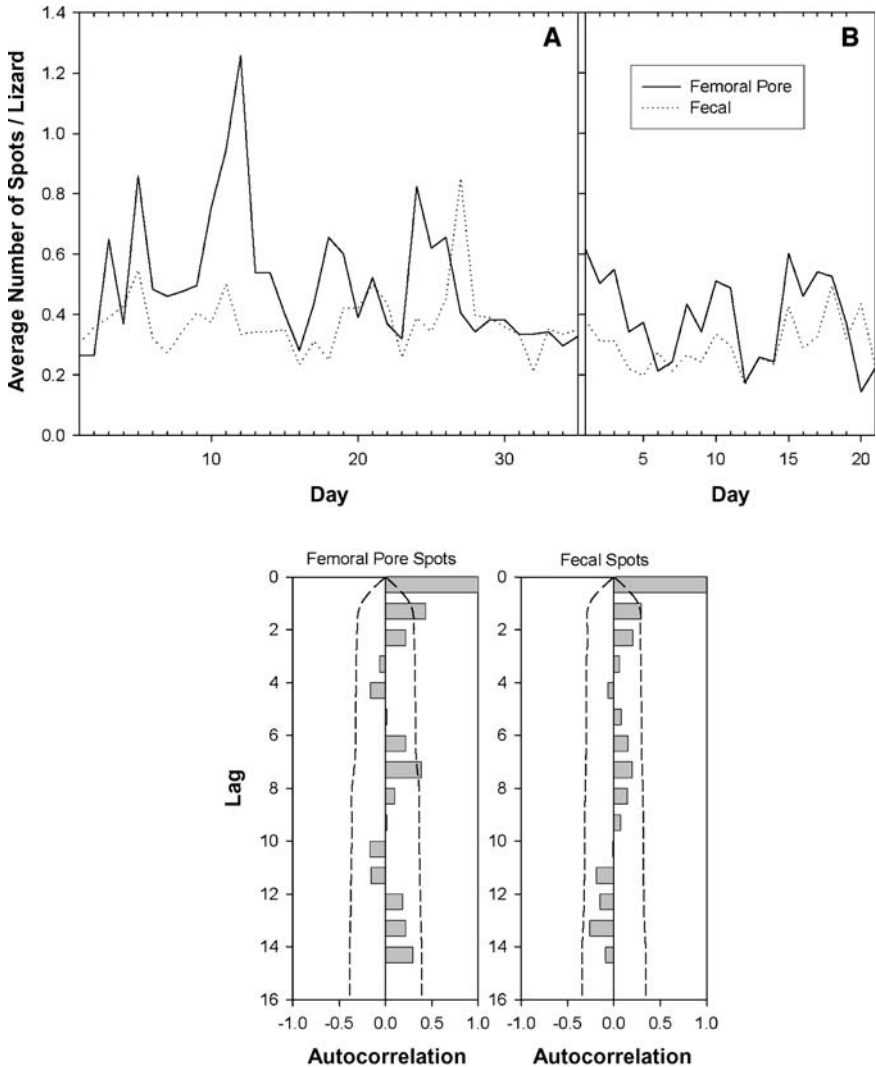
Fig. 3 Mean number of spots produced by lizards on each day of our study, averaging data for all male and female lizards. The first time sequence (A) was in October–November 2003, long after the mating season had ended. The second time sequence (B) was in January and February 2004, after animals emerged from hibernation and were beginning to show signs of reproductive activity. (C) Autocorrelation function (ACF) plots for the two time series describing relationships between the number of spots produced on different days. Bars show the magnitude of correlation coefficients calculated between the graphed data and the same time series shifted by a specified lag (up to 16 d). Dashed lines show 95% confidence intervals around a correlation of zero

territorial season (2003), but was strongly correlated with fecal spots during the subsequent mating season (2004).

Finally, assuming that lizards were synchronized with each other, time series analyses identified a cyclical pattern to the number of spots deposited, with lizards decreasing and then increasing the number of femoral pore and fecal spots produced each day (Fig. 3). This cyclical variation could be seen in the autocorrelation plots for the number of femoral pore spots, with significant positive autocorrelations at lags 1 and 7 ($r = 0.4$), with an intervening dip into negative autocorrelations at an intermediate lag 4 ($r = -0.2$). The pattern for fecal spots was similar, though weaker (autocorrelation $r = 0.2$ and 0.3 at lags 1 and 7, $r = -0.1$ at lag 4). With a series of relatively short duration (56 d), a first-order autoregressive model offered a sufficient fit to both femoral pore and fecal spot data, yielding the lowest BIC scores despite retaining much of the autocorrelation in the data.

Synchronization seems to have been stronger after hibernation than before. On days in which lizards produced more FPS, lizards also tended to produce larger spots, but this relationship was stronger during the mating season ($r = 0.7$, $P < 0.001$) than during the territorial season ($r = 0.4$, $P < 0.02$). Although there was no relationship between fecal spot number and size during the territorial season ($r < 0.1$, $P > 0.05$), the relationship was stronger but still not significant ($r = 0.35$, $P < 0.2$) during the mating season. The number of pore spots and the number of fecal spots produced by individual lizards on each day of the study were temporally linked during the mating season ($r = 0.5$, $P < 0.02$), but not before ($r = 0.2$, $P > 0.05$). There were no significant relationships between areas of femoral pore and fecal spots in either season.

Discussion

The results suggest that the amount of secretion deposited by lizards on a single perch may be an important component of the overall chemical signal, offering information on resident activity and physiological condition. The quantity of chemical deposits differed among animals of different body sizes and among animals in different part of their reproductive cycles. Deposits also varied on a weekly cycle, such that their degradation may convey information about resident lizard activity. Interestingly, a lizard could potentially gather this information from a distance, seeing as well as smelling the FPSs (Alberts, 1993). We found little difference between the sexes in the amount of chemical deposits, and no relationship between the amount of deposit produced by the same animal on different days or in different seasons of the year, suggesting that scent-marking behavior is not a good indicator of individual or sexual identity.

We found a discrepancy between gland production and chemical deposition on a single perch. Reproductively active males deposited fewer secretions than did females or territorially aggressive males, despite the known positive influence of androgens on gland productivity (Wade et al., 1993; Lindzey and Crews, 1993). This apparent contradiction can be resolved by recognizing that male sagebrush lizards are considerably more active than females, especially during the mating season, when most males defend several basking perches (Martins, 1991, 1993). Reproductively active rodents scent-mark more locations than do animals in other contexts (Wolff et al., 2002; Ferkin et al., 2004). Similarly, in a natural context, the extra

chemical secretions produced by sagebrush lizards during the mating season may be used to mark more locations rather than to mark any single location more heavily.

In mammals, seasonal increases in scent marking have been interpreted as support for the hypothesis that scent marks are used to advertise individual identity, especially at times in the seasonal cycle (i.e., mating season) when such information may be particularly important (Wolff et al., 2002; Ferkin et al., 2004). Our results extend the advertisement hypothesis by suggesting that the amount of deposition may convey information about physiological condition that supplements the information conveyed by the chemical structure of the signal. Thus, the amount of deposition may be an important element of the chemical signal, providing information about physiological condition and influencing the outcome of mate choice and aggressive interactions. We know that experimental manipulation of chemical cues on a lizard's skin alters its recognition by conspecifics (López and Martín, 2002), and the addition of femoral pore secretions to a robotic lizard model changes the behavioral response in playback experiments (Thompson, 2002). Playback studies are now also needed to determine whether receivers (lizard or mammal) can interpret effectively the information on physiological condition contained in deposit quantity.

The weekly cycle of scent-mark deposition also supports the hypothesis that femoral pore secretions function as territorial markers. Unlike in rodents, however, deposits were remarkably infrequent, with some lizards allowing several weeks to pass before depositing again, despite our daily removal of chemical secretions. Although it seems likely that the weekly cycle is required for replenishing a constant signal, further research is needed to determine whether, and how quickly, the signal is degraded and the extent this degradation may relate to the weekly cycle of deposition. Although experimental blocking of olfaction did not affect home ranges of sleepy lizards (Zuri and Bull, 2000), further studies of this sort with other lizard species may reach different conclusions. Most lizards maintain relatively exclusive territories despite considerable overlap in home ranges (Sheldahl and Martins, 2000) and behave differently when placed in an enclosure that has been previously occupied by other lizards (Labra et al., 2001). There also appears to be a relationship between the use of chemical secretions and the territorial headbob displays (Hews and Benard, 2001). Thus, experimental manipulation of olfaction with more targeted measures of changes in territory defense may yield further insights.

Finally, we found little evidence that lizards can determine individual identity, sex, or species of other animals from the quantity of chemical deposits. It seems more likely that differences in chemical composition of secretions among individuals, sexes, populations, and species (Alberts et al., 1993; Escobar et al., 2001) are used by lizards to distinguish sex, social status, and individual identity of conspecifics (Labra et al., 2001; López and Martín, 2001; Bull and Lindle, 2002; Aragón et al., 2003). We did not observe consistent individual differences in chemical deposition, as would be expected if secretion quantity were an indicator of individual identity. Moreover, an individual lizard's deposition during the prehibernation territorial season was not a good predictor of deposition during the posthibernation mating season. Further studies varying the amount and chemical composition of secretions or determining the amount of secretions produced in response to particular types of conspecifics are needed to confirm their use as territorial markers and communicative signals.

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