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Increased Predation Risk Modifies Lizard Scent-Mark Chemicals

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ABSTRACT Variation in environmental factors plays a central role on organisms' physiological changes. However, the physiological response to predation risk has rarely been investigated in reptiles. Chemical senses are important for intraspecific communication in squamate reptiles. In male lizards *Iberolacerta cyreni* the maintenance of relative proportions of lipids in femoral gland secretions is costly, which may ensure honest signalling of quality. We hypothesized that increased predation risk should compromise the maintenance of such lipid proportions, as both a fear response and escaping behavior can have physiological consequences. We simulated predator attacks and found that relative proportions of lipids in femoral gland secretions changed in disturbed lizards but not in control ones. Thus, predator–prey interactions may modulate relative concentrations of chemicals in scents of lizards. Potential consequences of this effect on intraspecific chemical communication are suggested. *J. Exp. Zool. 309A:427–433, 2008.* © 2008 Wiley-Liss, Inc.

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There are many biotic and abiotic factors inducing phenotypic plasticity in organisms to cope with potential deleterious effects of unpredictable environmental variation (Agrawal, 2001). Stressful situations such as starvation, inclement weather, increased predation pressure or agonistic interactions can modulate some aspects of the physiology in birds (Lynn et al., 2003), fish (Oliveira et al., 2001) and reptiles (Romero and Wikelski, 2001). These induced physiological responses may lead to subsequent changes that encompass from other physiological changes, such as mobilization of stored energy reserves, to complex behaviors, such as facultative dispersal (reviewed in Wingfield et al., '98; Dufty and Belthoff, 2001). Predation risk is considered as one of the most important forces modulating life history, morphological and behavioral traits (Agrawal, 2001; Benard, 2004; Martín and López, 2004). However, physiological changes in response to predation risk have rarely been investigated directly in vertebrates (but see Ylönen et al., 2006).

In squamate reptiles, chemical senses are important for intraspecific communication (Halpern, '92; Mason, '92; Cooper, '94; Schwenk, '95). The presence and relative concentrations of chemical compounds vary between individuals (Alberts, '90; '93), and can play a variety of functions in chemical communication (Cooper, 2004; Martín and López, 2006a). It has been shown that chemical composition of femoral gland secretions can be seasonally and status-dependent (Alberts et al., '92a,b). However, the contribution of phenotypic plasticity, in its broad sense of environmentally affected phenotypes, to this variation induced by biotic factors remains unclear.

The Iberian rock-lizard (*Iberolacerta cyreni*) is a small diurnal lacertid lizard found mainly in rocky habitats of some high mountains of the Iberian Peninsula. Lizards are active from May–October, mating in May–June and producing a single clutch

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in July (Elvira and Vigal, '85). In this species, scent-marks play an important role as home range advertisement and spacing behavior (Aragón et al., 2001a, 2006). Chemicals arising from femoral gland secretions are involved in social communication. For instance, male *I. cyreni* are able to discriminate between their own femoral gland secretions and those of familiar and unfamiliar conspecifics (Aragón et al., 2001b). More specifically, relative concentrations of lipids in femoral gland secretions may give reliable information on adult male traits used in sexual selection processes by other males (Martín and López, 2007) and by females (López et al., 2006; Martín and López, 2006a,b). Therefore, the variation of scent-marks' characteristics should have important consequences on intraspecific chemical communication in this species.

In male *I. cyreni* the maintenance of relative proportions of lipids in femoral gland secretions, used to scent mark substrates, may be costly, which therefore may ensure honest signalling of male quality (Martín and López, 2006b). In addition, it has been shown that both capture stress (Moore et al., '91) and physical activity (Gleeson and Hancock, 2002) to have physiological consequences in lizards. Therefore, we simulated predator attacks to test whether increased predation risk may constrain the maintenance of lipid proportions in femoral secretions of male *I. cyreni,* and to document, for the first time in reptiles, the effect of predation risk on chemical signals.

MATERIALS AND METHODS

Study species

Coinciding with the mating season on early June 2004, we captured by noosing 22 male *I. cyreni* at ''Alto del Telégrafo'' (Guadarrama mountains, Central Spain) at an elevation of 1990 m. Relative concentrations of chemicals in femoral gland secretions of lacertids may vary between adults and subadults (López and Martín, 2005a; Martín and López, 2006c). Therefore, only adult males were captured, as estimated from their body size (Elvira and Vigal, '85). We selected individuals of similar body size (weight: $\overline{X} \pm SE = 7.2 \pm 0.2$ g; snout-to-vent length (SVL): $\overline{X} \pm SE = 73.5 \pm 0.7$ mm) and with intact or fully regenerated tails, because metabolic rate can be affected by tail loss in lizards (Naya and Bozinovic, 2006). Lizards were individually housed at ''El Ventorrillo'' Field Station (Navacerrada, Madrid Province, Spain) 5 km from the capture site in outdoor opaque plastic cages (60 × 40 cm) containing a shelter. To prevent interacting effects between predation risk treatment per se and feeding rate as a by-product when availability of food is variable (Pérez-Tris et al., 2004), feeding was limited to one *Tenebrio molitor* larvae of similar size every day. We ensured that all lizards ate the larvae each day. The same amount of water was provided for each lizard. In addition, to standardize potential costs of refuge use during captivity (Amo et al., 2007a), all individuals had access to one shelter of similar size and shape. All lizards were measured and weighed before and after the experimental manipulation.

Experimental manipulation

To minimize potential effects of captivity stress, all lizards were acclimated to their home cages during 2 days before the experimental manipulation. To assess the effect of increased predation pressure on the composition of femoral gland secretions, an equal number of males ($n = 11$ per treatment) were randomly assigned to two treatments: ''predation risk'' treatment and ''control'' treatment. In the ''predation risk'' treatment we simulated predation encounters by human attacks five times per day separated by 1.5 hr (09:00–15:00 hr GTM), during 7 days. Each predation encounter consisted in chasing lizards by hand tapping in the soil during 30 sec, but no lizard was actually touched during chases. To avoid handling effects, chasings were performed in the lizard's home cages after gently removing shelters, which were replaced after trials. Similar procedures have been recurrently used in other lizard studies to simulate increased predation risk in the environment (e.g. Pérez-Tris et al., 2004; Amo et al., 2007b). Control males were held under the same conditions but they were not disturbed. All lizards were returned healthy to their capture sites.

Chemical analyses of femoral secretions of males

Femoral gland secretions of males were extracted before (on the capture date) and 1 day after the experimental manipulation, by gently pressing with forceps around the pores. Blank control vials were treated in the same manner to examine the presence of potential contaminants and compare them with the lizard samples. Secretions were collected in glass vials with Teflon-lined stoppers (Wilmington, Delaware) and stored at -20°C until analyses. Samples were analyzed with a Finnigan-ThermoQuest Trace 2000 gas chromatograph (Austin, Texas) fitted with a poly (5% diphenyl/95% dimethylsiloxane) column (Supelco, Equity-5, 30 m length × 0·25 mm ID, 0·25 μm film thickness) and a Finnigan-ThermoQuest Trace mass spectrometer as detector. The oven temperature was programmed at 50°C for 10 min, then increased to 280°C at 5°C min^{-1} and kept at 280°C for 30 min. Identification of compounds was done by comparison of mass spectra in the NIST/EPA/NIH 1998 library and later confirmed with authentic standards (see López and Martín, 2005b; López et al., 2006 for a more detailed description of analytical methods and chemical compounds in femoral secretions of this species).

The relative amount of each component was determined as the percent of the total ion current (TIC). Then, we selected the 18 major peaks that represented $>0\cdot1\%$ relative peak area (which together represent 98% of total TIC area) and that were present in all the individuals to reduce the number of variables to be used in the statistical analysis (Dietemann et al., 2003). Other minor components (TIC area $<0.1\%$) were not found in every individual, probably owing to difficulties in detecting trace components in all samples. Thus, these compounds were not considered in further tests. However, average frequencies of appearance of minor components were similar in control and experimental lizards. The relative areas of the selected major peaks were restandardized to 100% and transformed following Aitchison's formula: $[Z_{ij} = \ln(Y_{ij}/g(Y_j)]$, where Z_{ij} is the standardized peak area i for individual j, Y_{ij} is the peak area i for individual j, and $g(Y_j)$ is the geometric mean of all peaks for individual j (Aitchison, '86; Dietemann et al., 2003). The homogeneity of variance of these variables was tested with Levene's test, and Bonferroni's correction was applied. The transformed areas were used as variables in a principal component analysis (PCA).

Data analyses

All factors (PCs) obtained from the PCA were used as potential predictors. To test whether there were differences in relative proportions of chemical compounds before and after the experimental manipulation we use multivariate analysis of variances (MANOVAs) including all PCs. When a significant effect was found in the multivariate analyses we used protected repeated measures analysis of variances (ANOVAs), with time (before and after treatment) as a within-subject factor. For PCs that significantly changed in disturbed lizards, same test was performed for control individuals to verify that the effect was not owing to the progress of the season or captivity. Normality and homogeneity of variances were verified by the Kolmogorov–Smirnov test and Levene's test, respectively. For the repeated measures models, sphericity was not checked because all the within-subjects factors have only two levels and therefore each variance–covariance matrix is a vector (Quinn and Keough, 2002).

To test for effects of captivity time, progress of the season or experimental manipulation on morphometric traits (SVL, body mass and corpulence) we used univariate one-way ANOVAs. Corpulence was used as a relative measure of weight and was estimated by taking the residual score of the linear regression of the body weight on the SVL. Unadjusted probabilities are reported, but significance was verified using the sequential Bonferroni adjustment for each family of tests (Chandler, '95).

RESULTS

Individual morphometric traits

Morphometry did not differ significantly between control and disturbed males before (SVL: $F_{1,20} = 0.02$, $P = 0.89$; body mass: $F_{1,20} = 0.85$, $P = 0.36$; corpulence: $F_{1,20} = 1.86$, $P = 0.18$) or after the treatment execution (SVL: $F_{1,20} = 0.20$, $P = 0.65$; body mass: $F_{1,20} = 0.006$, $P = 0.93$; corpulence: $F_{1,20} = 0.13$, $P = 0.72$). Similarly, there were no significant differences in the change in morphometric traits, estimated as the difference between each trait before and after the experimental manipulation (SVL difference: $F_{1,20} = 1.03$, $P = 0.32$; body mass difference: $F_{1,20} = 2.07$, $P = 0.16$; corpulence difference: $F_{1,20} = 2.88$, $P = 0.10$). No lizard lost its tail during the experimental procedures.

Variation of chemical proportions in gland secretions

Eighteen major chemical compounds were identified in femoral gland secretions (Table 1). PCAs produced five PCs, which together accounted for 70.11% of the total variance. All PCs had eigenvalues higher than 1 (Table 1). There were no significant differences between lizards in the "control" and "predation risk" treatments before the beginning of the experimental manipulation (MANOVA: Wilk's $\lambda = 0.77$, $F_{5,16} = 0.90$, $P = 0.49$).

TABLE 1. Principal components analysis for relative proportion of chemicals in femoral gland secretions of male lizards

Compound	PC-1	PC-2	PC-3	PC-4	PC-5
Dodecanoic acid	−0.47	**0.64**	−0.15	−0.39	−0.02
Hexadecanoic acid	**−0.77**	−0.05	0.07	0.42	−0.14
Octadecenoic acid	−0.07	0.20	0.03	**−0.79**	0.12
Octadecanoic acid	**−0.76**	0.01	0.19	−0.20	0.25
Squalene	−0.13	−0.01	0.33	**−0.77**	0.11
Cholesterol	0.14	**0.71**	−0.36	−0.11	−0.11
Cholesta-5,7-dien-3-ol	−0.24	0.49	−0.25	−0.29	0.20
Ergosta-7,22-dien-3-ol	−0.10	0.21	**−0.85**	0.02	0.13
Ergosterol	0.01	−0.06	**−0.86**	0.21	−0.04
Stigmasta-5,24(28)-dien-3-ol	−0.07	**0.75**	0.08	0.09	0.06
Campesterol	**0.76**	−0.02	0.18	0.38	−0.17
Ergosta-5,8-dien-3-ol	**0.57**	−0.39	0.31	0.01	0.28
Lanost-8-en-3-ol	0.13	0.00	−0.11	0.06	**−0.70**
2,2-Dimethyl-cholest-8(14)-en-3-ol	0.15	0.20	−0.09	0.48	**0.50**
Sitosterol	**0.66**	−0.01	0.19	**0.53**	−0.13
24-Propylidene-cholest-5-en-3-ol	0.06	0.16	0.28	0.30	**−0.70**
4,4-Dimethyl-cholesta-5,7-dien-3-ol	0.11	**−0.81**	0.07	0.29	0.19
Unidentified waxy ester	−0.16	**−0.69**	−0.13	−0.28	−0.06
Eigenvalue	4.54	2.96	2.06	1.72	1.32
% Variance	25.23	16.45	11.48	9.58	7.37

Bold lettering denotes factor loadings higher than 0.5.

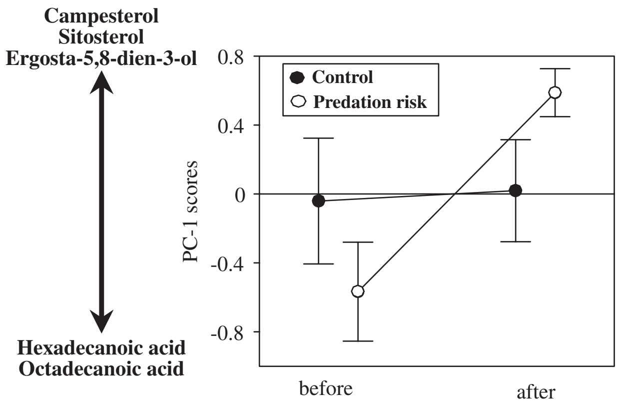

Fig. 1. PC-1 scores (mean ± SE) before and after simulated predator attacks and in control males. PC-1 is extracted from the factor analyses for relative proportions of chemicals in femoral gland secretions of male lizards.

In contrast, after the treatment, the relative proportions of chemicals in secretions of disturbed lizards were significantly different from control males (Wilk's $\lambda = 0.47$, $F_{5,16} = 3.53$, $P = 0.024$). PC-1 scores were significantly higher after the simulated chasings in disturbed lizards (repeated measures ANOVA: $F_{1,10} = 13.61$, $P = 0.004$; Fig. 1), whereas there was no significant effect for control individuals ($F_{1,10} = 0.01$, $P = 0.90$). Thus, proportions of two carboxylic acids (hexadecanoic and octadecanoic acid) decreased, whereas proportions of three steroids (campesterol, sitosterol and ergosta-5,8-dien-3-ol) increased in disturbed lizards. (Fig. 1; Table 1). There were no significant effects of chasings for the other PCs after Bonferroni correction (PC-2: $F_{1,10} = 2.38$, $P = 0.15$; PC-3: $F_{1,10} = 0.001$, $P = 0.97$; PC-4: $F_{1,10} = 2.37$, $P = 0.15$; PC-5: $F_{1,10} = 6.34$, $P = 0.03$).

DISCUSSION

Our manipulation induced a change in relative proportions of chemicals in femoral gland secretions of male lizards, but the treatment was not strong enough to provoke significant changes in morphology. In contrast, chasings provoked loss of body mass in other lacertid species in natural (Martín and López, '99) and captive conditions (Pérez-Tris et al., 2004). Interestingly, previous studies with *I. cyreni* showed that the level of predation risk in natural conditions may be either associated (Amo et al., 2007b) or not (Amo et al., 2007a) with changes in body mass depending on season and environmental variables. In our experiment, we held fixed potential sources of variation in nature that might act additively or synergistically with simulated predator attacks to account for an effect on loss of body mass. For instance, it is known that the growing rate is asymptotically age-dependent in lacertids (e.g. Roitberg and Smirina, 2006) and, hence, a lower variability in morphometry is expected for older males. As composition of femoral gland secretions in lacertids may vary between adults and subadults (López and Martín, 2005a; López and Martín, 2006), in our study we only selected adult males to reduce variation in relative proportions in chemicals. Therefore, further studies are necessary to examine whether this variability in the effect of predation risk on the body mass found among and within lizard species arises because of different levels of predation risk in the experimental design, different ranges of age, variation in food intake or taxonomic differences. Whatever the key difference between this and previous studies, our study suggests that the physiological flexibility (Piersma and Drent, 2003) found here is not linked with the loss of body mass.

Although explaining the underlying physiological mechanism mediating the observed changes is beyond the scope of the present experiment, at least two nonexclusive potential mechanisms can be argued. It is well established that stressful situations may lead to an increase in circulating corticosterone in vertebrales (Sapolsky et al., 2000; Lynn et al., 2003). The observed changes owing to simulated predation risk might be induced by the fear stimuli as it has been shown that handling by humans may provoke a rise in corticosterone levels in birds (e.g. Silverin et al., ’97; Silverin and Wingfield, ’98) and reptiles (lizards: Moore et al., ’91; snakes: Moore et al., 2000). Glucocorticoids regulate lipid and steroid metabolism in a variety of vertebrates (Assenmacher, ’73; Wade and Schneider, ’92; Bjorntorp, ’96), including poikilothermic vertebrates (Sheridan ’94). More specifically, it has been demonstrated that corticosterone levels produced by stressful situations are associated with the rapid change of free fatty acid concentrations (Palokangas and Vihko, ’71; Harris et al., ’94). Thus, the changes in free fatty acid concentrations in the current experiment might reflect that increased predation risk also increased stress levels.

An alternative but nonexclusive potential mechanism is that the observed changes might not be merely owing to the fear stimuli but a product of increased physical activity per se. For instance, it has been shown that the metabolic costs associated with short and intense activity in the lizard *Dipsosaurus dorsalis* are large enough to impact the energy budget (Hancock et al., 2001). Thus, the antipredatory response to predator attacks by means of escaping behavior can have significant consequences when there is a high predation pressure in natural conditions. Whatever the type of mechanism involved, the current experiment shows that changes in free fatty acid concentrations produced by simulated predation attacks may also be reflected in gland secretions used as chemical signals. Further studies will be needed to determine the trigger of the observed changes.

The fatty acids found in the femoral gland secretions in this study have already been described in previous studies of this species (López and Martín, 2005b) and in other Lacertid species (López and Martín, 2005a,c, 2006; Martín and López, 2006c,d) and also in Iguanid lizards of the genus *Liolaemus* (Escobar et al., 2001) and *Iguana* (Alberts et al., ’92). Carboxylic acids found in femoral secretions of *I. cyreni* range from n-C_6 to n-C_{22}, and their relative concentrations vary among individuals (López and Martín, 2005b). The variability in chain length of carboxylic acids in gland secretions should be linked with pheromonal volatility (Alberts, ’92). In concordance, it has been argued for lizard species that the range of carbon atoms number appropriately matches with the ambient temperature because the interaction of both parameters affects volatility of scents in the substrate (Escobar et al., 2003; López and Martín, 2005b). However, interpopulational or habitat differences in carboxylic acids previously reported did not disentangle whether the origin of this variability is owing to genetic diversity, phenotypic plasticity or both (Escobar et al., 2003; Martín and López, 2006d). Our results showed that this variation may be achieved, at least in part, through physiological flexibility caused by a biotic factor.

The influence of predation risk on chemical proportions might have important consequences in the efficiency of intraspecific chemical communication of squamate reptiles as previous evidence supports that lipids are involved in chemical signalling (e.g. LeMaster and Mason, 2001; López and Martín, 2005c; Martín and López, 2006a,b). For instance, a potential cost related to signalling male quality may be involved. Previous studies revealed that relative proportions of lipids in femoral secretions may be reliable advertisements of male quality, which females may use to select mates (López and Martín, 2005c; Martín and López, 2006a,b; López et al., 2006). More specifically linked to our results, relative proportions of lipids such as hexadecanoic acid are negatively correlated with fluctuating asymmetry levels of male *I. cyreni* (López et al., 2006). A trait that is used by females in sexual selection processes, being scents of symmetric males more attractive to female *I. cyreni* (Martín and López, 2000). Interestingly, our results showed a decrease in relative proportions of hexadecanoic acid under simulated increased predation risk. Thus, it can be argued that those males that better afford this constraint induced by stress of predation, would be more attractive to females. Our results highlight the need for further studies to examine the complexity of physiological changes and biotic interactions, and their fitness consequences, which would enable us to prevent ecological perturbations, such as introduction of predators or human disturbance.

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