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Abstract

We examined the selective consequences of variation in behaviour and endocrine physiology in two female throat-colour morphs of the lizard, *Uta stansburiana* in the wild. Female morphs differed in home-range distribution patterns and corticosterone levels in relation to the density and frequency of their female neighbours. Levels of plasma corticosterone of yellow-throated females increased with increased density of both morphs. In contrast, orange-throated females had reduced levels of corticosterone in response to increased density of orange females. Additionally, females with lower corticosterone survived poorly, suggesting that social interactions and high local densities of orange females may be potentially costly for orange females. These results are consistent with decreased fitness effects and suppression of immune function previously reported for orange female morphs surrounded by more orange neighbours. These correlations, in conjunction with previous work in this system, indicate that corticosterone is likely to be an important physiological mechanism regulating female fitness in nature.

Introduction

A major challenge in evolutionary biology is to understand the selective factors and proximate mechanisms that generate and maintain phenotypic variation. In the study of life history evolution, examination of species with conspicuous, heritable polymorphisms has elucidated some of the interactions between social competition, hormonal regulation and phenotypic plasticity (West-Eberhard, 1989; Ketterson & Nolan, 1992; Sinervo *et al.*, 2000a; Svensson *et al.*, 2002). However, several factors regarding morphs remain unresolved. For example, we have only a basic understanding of the ecological factors that maintain polymorphisms, the physiological and developmental mechanisms underlying morphotype differentiation, and how the interaction between genotype and environment affects morph

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fitness (Moore *et al.*, 1998; Svensson *et al.*, 2002). Our lack of knowledge is in large part due to the tremendous difficulty of investigating these mechanisms in nature. Here, we begin addressing the evolutionary consequences of hormone action by describing the role of plasma corticosterone in modulating social competition during reproduction and examining the correlation between corticosterone and survival in free-ranging female morphs of the side-blotched lizard, *Uta stansburiana*. We investigated the physiological and selective consequences of natural corticosterone levels to explore the proximate basis of behavioural strategies and life history trade-offs.

Hormones are a mechanistic link between the social environment, behaviour and reproductive success (Moore & Marler, 1988). One way the social environment strongly influences behaviour and reproduction is through the release of glucocorticoids (Wingfield & Ramenofsky, 1999). For example, individuals undergoing disruption in social ranks or involvement in agonistic behavioural encounters frequently have elevated corticosterone levels (the primary glucocorticoid

in reptiles, birds and many rodents; Sapolsky, 1987; Schwabl, 1995; Wingfield & Ramenofsky, 1999; Creel, 2001). There is considerable variation in how individuals and species respond to stressors and how these adjustments lead to changes in behaviour and physiology (Astheimer et al., 1992; Munck et al., 1994; Knapp & Moore, 1996; Knapp & Moore, 1997). In the case of frequency-dependent selection, local social interactions between individuals of different morphotypes can generate strong effects on both physiology and fitness (Brandon, 1990; Sinervo et al., 2000a; Svensson et al., 2001a,b). It is likely that these fitness effects are largely mediated by the endocrine system (Sinervo & Svensson, 1998).

Acute and chronic corticosterone responses differ greatly in their consequences. During the acute response, on the time scale of hours to days, corticosterone levels generally increase several fold and cause a shift in energy away from physiological processes unnecessary for immediate survival (Ingle, 1952; Munck et al., 1994). Increases in corticosterone trigger a set of alternative behaviours (emergency life history stage) that work to minimize the effects of stressors (Wingfield et al., 1998). When corticosterone remains elevated at high levels for longer periods of time (weeks to months), a wide range of negative consequences can occur, including reproductive suppression (Sapolsky, 1992), reduced immunocompetence (Munck et al., 1994), decreased insulin production and neural degeneration (Bremner, 1999).

In contrast to extreme stressors and chronically high levels of corticosterone, which inhibit reproduction, some field studies have shown a positive relationship between baseline corticosterone levels and reproductive activity (reviewed in Greenberg & Wingfield, 1987). In free-living populations of the side-blotched lizard, corticosterone levels are higher during vitellogenesis indicating that corticosterone affects egg production or oocyte maturation (Wilson & Wingfield, 1992). When administered early in vitellogenesis, exogenous corticosterone increases clutch mass investment (Sinervo & Denardo, 1996). Thus, corticosterone is likely to be a key physiological mechanism regulating life history trade-offs in nature.

Here, we present results from a field study on the effects of the female social environment on corticosterone levels and investigate the relationship between corticosterone level and survival during reproduction. By combining detailed analysis of home range maps with field endocrinological data, we demonstrate that each female morph shows a different corticosterone profile in relation to the presence of female neighbours. Thence, we combine analysis of alternative female reproductive strategies, socio-endocrinology and the consequences of endocrine regulation for survival in a free-living population.

Materials and methods

Study organism and demographic cycles

The side-blotched lizard, a small (4–10 g) phrynosomatid lizard, matures in 1 year and in the study population individuals rarely survive more than one reproductive season (Sinervo & Denardo, 1996). Females lay multiple clutches at monthly intervals ranging from April to August. Both males and females have home ranges and hatchling dispersal is limited (Doughty & Sinervo, 1994). Approximately 10 days prior to ovulation, females express orange or yellow throat coloration (heritability = 0.48; Sinervo et al., 2000a).

Previously, we have demonstrated that the female morphs have different reproductive strategies (Sinervo et al., 2000a). Orange females lay large clutches of small eggs and individual fitness is more sensitive to local density than it is for yellow females that lay small clutches of large eggs (Sinervo et al., 2000a). The number of breeding females in this population has oscillated in synchronous, 2-year cycles (Sinervo et al., 2000a). Selection gradients on egg mass and clutch size, survival of progeny, and frequency of female colour morphs follow concordant oscillations with population cycles (Sinervo et al., 2000a). In addition to the correlation between female morphotype and life history traits, we have also demonstrated that female morphotype is associated with physiological measures of condition, including immunocompetence and post-laying mass (Svensson et al., 2001a).

Field work was conducted between March 1 1998 and August 30 1999 in a free-ranging population of side-blotched lizards, U. stansburiana, on Billy Wright Road, Merced County, CA, USA. Each individual in the population was permanently marked with unique toe-clips and painted on the dorsum with small, temporary symbols to facilitate identification during home range mapping (see below).

Measurement of local social environment

During the breeding season females and males inhabit rocky outcroppings of sandstone, which function as discrete social neighbourhoods due to their separation from other outcroppings by unoccupied, grassy areas. The habitat structure, limited movement of individuals, and the necessity for lizards to behaviourally thermoregulate (bask in conspicuous well-lit locations) make it possible to catch every lizard in the population (Sinervo et al., 2000a). Locations of individual females were mapped during vitellogenesis of the first clutch (from March 1 to April 30; mean observations per female = 7.52; SE = ±0.52) and survival to subsequent clutches was assessed through August. Home range areas were computed from minimum convex polygons,

circumscribing all mapped locations for each female. We quantified a female's social environment as the number of neighbouring orange and yellow females with intersecting home ranges.

To further examine spatial distribution of female morphs, we examined how the morphs were distributed with respect to several social categories. Females were categorized as either having no neighbours (solitary) or having one or more neighbours. Then, if a female had a neighbour, we examined the proportion of neighbours that were orange. To increase sample size for this spatial analysis, we used an expanded data set that included females with experimentally manipulated clutch size (Svensson *et al.*, 2002). The majority of home range data were collected prior to clutch size manipulations and there was no effect of treatment on the number of orange neighbours (ANOVA; $F_{1,100} = 0.86$; $P = 0.43$), the number of yellow neighbours (ANOVA; $F_{1,100} = 1.00$; $P = 0.37$) or total female density (ANOVA; $F_{1,100} = 1.07$; $P = 0.35$).

Validation of the stress response

We conducted a test to measure the magnitude of the acute stress response. Ten females from outside the study plot were captured and bled at three time intervals: (i) immediately after capture to measure baseline corticosterone levels, (ii) after 30 min of handling, and (iii) after 60 min of handling. Samples were collected after the breeding season when throat colour was not expressed, and therefore we were not able to address the relationship between female morph and stress response. Although it is possible that the stress responses can differ in magnitude between nonbreeding and breeding individuals (Jessop *et al.*, 2002), this test was carried out to confirm that corticosterone is released during acute stress and the range of the response in this species. In addition, this test serves as a validation of the radioimmunoassay protocol.

Measurement of survival

Survival was assessed by recapture and daily observation over two time periods: (i) from the beginning of the breeding season to the production of the first clutch (March–May) and (ii) between the first and second clutch (May–August). A total of 167 and 200 females were captured at the start of the breeding season in 1998 and 1999, respectively. There were no significant between-year differences in survival to first reproduction (logistic regression; $\chi^2_{(1)} = 0.08$; $P = 0.78$) or in survival to the second clutch (logistic regression; $\chi^2_{(1)} = 1.89$; $P = 0.17$).

Subsequent to blood sampling, females were brought into the laboratory to lay eggs [14 ± 1 (mean ± SE) days in laboratory]. After ovipositing their eggs, females were released at the site of capture. Females readily reestablish residency on their home range. From May to June, survival to the second clutch was determined by home range monitoring and subsequent recaptures. Survival rates on a control outcrop where individuals were not brought into the laboratory to lay eggs were similar to those on our intensively studied outcrops (Sinervo & Denardo, 1996; Sinervo *et al.*, 2000a).

Reproductive status, collection of blood samples and radioimmunoassays

Ovulation status is reliably determined by abdominal palpation (Sinervo & Licht, 1991). Females were captured throughout the season to determine reproductive status [3.89 ± 0.152 (mean ± SE) recaptures per female]. Shortly after ovulation, blood samples were taken from the post-orbital sinus using two to three 50-μL haematocrit tubes (Sinervo *et al.*, 2000b). We measured catch time (average = 59 ± 20 s; range 8–266 s) and total handling time (average = 166 ± 21 s; range 77–1120 s) between capture and termination of blood collection to verify that handling stress did not affect corticosterone levels (see Results). Ninety per cent of the samples had a total handling time <300 s. Samples were kept on ice for 4–6 h before centrifugation after which plasma was extracted and frozen at −20 °C until steroid assay.

Circulating levels of corticosterone and progesterone were determined by radioimmunoassay (Wingfield *et al.*, 1992). Progesterone covaries with ovulatory status and furthermore progesterone levels affect corticosterone. Accordingly, we removed the effect of ovulation status by using progesterone as a covariate in all analyses. We used 10 μ L^{-1} of plasma for direct corticosterone assays and 20 μ L^{-1} for direct progesterone assays. Samples were combined with radiolabelled steroid for calculation of percentage recovery, extracted with freshly decanted dichloromethane (ethyl ether used for progesterone) and evaporated with nitrogen in a 40 °C water bath. Samples were reconstituted with buffer, placed in duplicate vials, and competitive binding was accomplished by adding radiolabelled steroid and corticosterone antiserum (Endocrine Sciences, Calabasas Hills, CA, USA). Dextran-coated charcoal was used to absorb all unbound steroid; the supernatant was centrifuged and counted for bound radioactive corticosterone. Average percentage recovery of corticosterone and progesterone was 92.0 and 68%, respectively. Intra-assay variation remained below 15%.

Statistical analysis

We used ANCOVA, logistic regression and χ^2 analysis to evaluate the effect of throat colour and number of female neighbours of each morphotype on corticosterone levels and female survival. All analyses were performed using JMP (SAS Institute, 1989) and the alpha level was set at $P = 0.05$.

Results

Handling time and acute stress test

The time required to capture females in the field had no effect on corticosterone (ANCOVA; $F_{1,42} = 0.80$; $P = 0.38$) nor did the total handling time required from capture until the termination of blood collection in the field (ANCOVA; $F_{1,42} = 0.67$; $P = 0.42$).

However, with extensive handling, our stress test indicated that corticosterone levels increase dramatically (ANOVA; $F_{1,29} = 61.65$; $P = 0.0001$). The mean corticosterone levels measured after prolonged handling stress (mean = 217.16 ng ml^{-1} after 60 min) were nearly twice as high as the maximum levels we measured in naturally occurring corticosterone in this population (max = 116.30 ng ml^{-1}). In 1998 and 1999 the mean corticosterone values were 51.17 and 50.77 ng ml^{-1}, respectively. Mean progesterone values were 14.44 and 14.66 ng ml^{-1} in 1998 and 1999, respectively.

Social environment and corticosterone levels

Total local density has a marginal effect on corticosterone irrespective of morphotype (ANCOVA; $F_{1,38} = 3.07$; $P = 0.09$; see Table 1). When we accounted for the effect of the neighbour morphotype, we found that corticosterone levels increased with the number of yellow neighbours, both among orange and yellow females (Table 2: Fig. 1 a,c; $F_{1,35} = 8.468$; $P = 0.006$). The increase was more pronounced for orange females, although the interaction was not significant (Table 2: morph × yellow neighbour; ANCOVA; $F_{1,35} = 2.641$; $P = 0.113$). Corticosterone levels of orange and yellow females differed significantly in response to the local density of orange neighbours (Table 2: Fig. 1b,d; morph × orange neighbour; ANCOVA; $F_{1,35} = 5.108$; $P = 0.030$). Yellow females with more orange neighbours had higher corticosterone levels whereas orange females surrounded by more orange neighbours had decreased corticosterone levels.

Table 1 ANCOVA results for the effect of local density, year, throat morph and progesterone on corticosterone level. Local density and progesterone are continuous variables, and year and throat are factors. All higher order interactions involving covariates were not significant indicating the assumptions of homogeneity of slopes was met, and thus were removed from the model. The reduced model is presented here.

Source of variation	d.f.	SS	F ratio	P value
Total density	1	1573.338	3.069	0.087
Throat morph	1	139.641	0.272	0.605
Year	1	235.440	0.459	0.502
Progesterone	1	2028.999	3.959	0.054
Residual	38	19477.319		

SS = sum of squares.

Table 2 ANCOVA results for the effect of social environment (number of yellow neighbours and number of orange neighbours), progesterone, year and throat morph on corticosterone levels. Year and throat morph are factors, and progesterone and the number of orange and yellow neighbours are continuous variables. The two-way interactions with orange and yellow neighbours and throat morph are included in the model. There was a positive effect of the number of yellow neighbours and a significant interaction term between number of orange neighbours and morphotype, indicating that female morphs respond differently to the number of orange neighbours in their local environment. The reaction norm of orange females towards increasing number of orange females was negative whereas the reponse of yellow females had a positive slope.

Source of variation	d.f.	SS	F ratio	P value
Progesterone	1	3011.46	6.662	0.014
Year	1	66.271	0.0147	0.704
Throat morph	1	18.159	0.040	0.842
No. of yellow neighbours	1	3828.128	8.468	0.006
No. of orange neighbours	1	437.022	0.967	0.967
No. of yellow neigbours × throat morph	1	1193.850	2.641	0.113
No. of orange neigbours × throat morph	1	2308.896	5.108	0.030
Residual	35	22773.528		

SS = sum of squares.

Relationship between corticosterone and survival to the second clutch

Females that survived to lay a second clutch had significantly higher corticosterone levels at ovulation on the first clutch than those that did not survive to lay a second clutch (Table 3: logistic regression; $\chi^2_{(1)} = 5.971$; $P = 0.015$). Using a second model that included morphs and social environment as covariates, the effects of morph, social environment and their interactions were not significant, although the effect of corticosterone residuals remained significant (Table 4: logistic regression; $\chi^2_{(1)} = 6.722$; $P = 0.010$).

Spatial associations

We found that the female morphs differed with respect to social neighbourhoods. For yellow females ($n = 37$), there was no difference in the probability of being solitary or having neighbours (one or more), whereas orange females ($n = 30$) were less likely to be solitary than to have neighbours (Fisher's exact test: $\chi^2_{(1)} = 5.55$; $P = 0.02$). The morphs differed in the proportion of neighbours that were orange (ANCOVA; $F_{1,64} = 4.398$; $P = 0.04$), with no effect of total density ($F_{1,64} = 0.054$; $P = 0.817$) or interaction between morphotype and total density ($F_{1,64} = 1.956$; $P = 0.167$).

Discussion

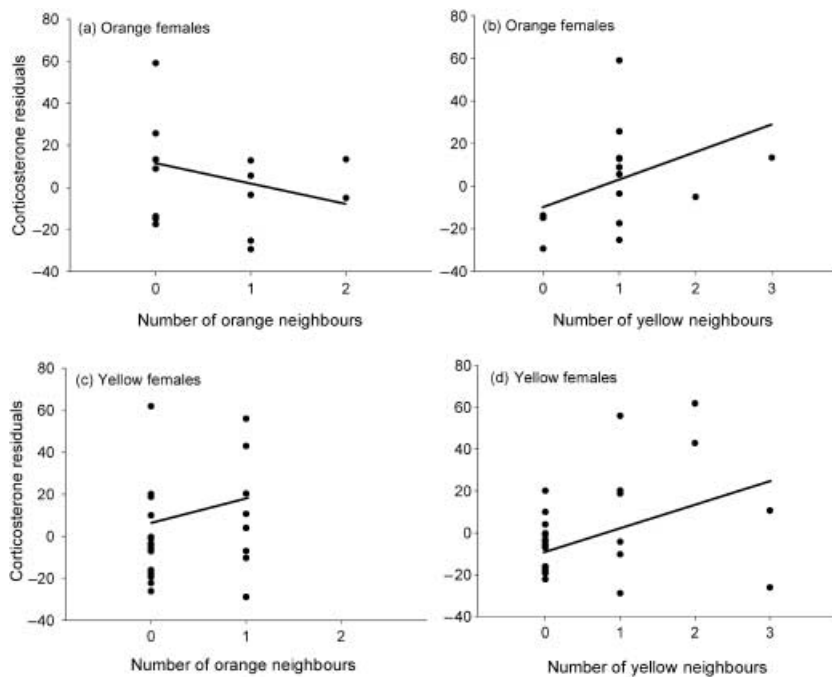In this study, we found that the two morphs had different corticosterone responses towards the local social

Fig. 1 Relationship between corticosterone levels [residuals, corrected for year and progesterone levels (ng mL^{-1})]. Positive values indicate high response and negative values, low response. (a and c) The slopes of the reaction norms towards the number of orange neighbours differ significantly between the two female morphs (ANCOVA: throat × number of orange neighbours; $F_{1,35} = 5.05$; $P = 0.03$). (b and d) There is a significant positive effect of the number of yellow neighbours on corticosterone response (ANCOVA; $F_{1,35} = 8.33$; $P = 0.007$).

Table 3 The results from a logistic regression with survial to the second clutch as the dependent variable, year and throat morph as factors, and progesterone and corticosterone as covariates. Corticosterone has a positive effect on survival to the second clutch.

Source of variation	d.f.	Wald χ^2	P value
Year	1	0.315	0.575
Throat morph	1	0.359	0.575
Progesterone	1	0.370	0.543
Corticosterone	1	5.971	0.015

Table 4 Logistic regression with survival to the second clutch as the dependent variable, year and throat morph as factors, progesterone, social environment and corticosterone as covariates. The three-way interaction (number of orange neighbours × number of yellow neighbours × throat morph) was not significant and was removed from the model. The reduced model is shown here. The positive effect of corticosterone persists when controlling for social factors.

Source of variation	d.f.	Wald χ^2	P value
Year	1	1.176	0.278
Throat morph	1	0.583	0.445
Progesterone	1	3.471	0.063
Corticosterone	1	6.722	0.010
No. of yellow neighbours	1	0.002	0.964
No. of orange neighbours	1	2.463	0.117
No. of yellow neigbours × throat morph	1	0.992	0.319
No. of orange neigbours × throat morph	1	2.501	0.114
No. of orange neigbours × no. of yellow neighbours	1	0.013	0.908

environment. Although other variables may be contributing to the observed variation in corticosterone levels, we found that the slopes of the corticosterone norms-of-reaction of orange and yellow females were different in response to the number of orange neighbours (Fig. 1). Orange females were more sensitive (i.e. plastic) with respect to how corticosterone changed in response to density and frequency of female neighbours. This interaction is consistent with previous morphotype-by-social environment interactions that we have uncovered for orange females in immune function (Svensson *et al.*, 2001a) and reproductive fitness (Sinervo *et al.*, 2000a). Orange females cannot maintain a high level of immunocompetence in the presence of crowding, particularly when crowded by females of their own morphotype (Svensson *et al.*, 2001a,b). Similarly, orange female fitness (survival of female progeny to maturity) collapses at high density of orange females; in contrast, orange female fitness rises at high density of yellow neighbours (Sinervo *et al.*, 2000a).

The acute handling experiment demonstrates that the baseline corticosterone levels, which are likely to be influenced by social interactions, are substantially lower than levels that occur during extreme stress. Although aspects of the social environment may increase or decrease corticosterone secretion, these adjustments occur within a baseline range that does not inhibit reproduction. At this scale, elevated levels of corticosterone can enhance resistance to stress, mobilize energy and thus improve the probability of survival. In both female morphs, corticosterone was positively related to survival
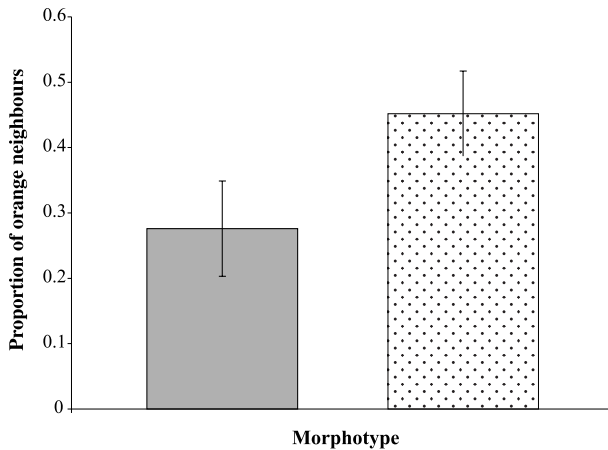
Fig. 2 Orange and yellow females differed in proportion of orange female neighbours (ANCOVA: $F_{1,64} = 4398$; $P = 0.04$), with no effect of total density ($F_{1,64} = 0.054$; $P = 0.817$) or interaction between morphotype and total density ($F_{1,64} = 1.956$; $P = 0.167$). Orange females had a lower proportion of orange female neighbours than yellow females.

to the second clutch. Therefore, the interaction between female morphotype and number of orange neighbours suggests that the inability of orange females to maintain elevated levels of corticosterone may have direct negative fitness consequences.

These endocrine data suggest that orange females are under strong selection pressure to have fewer orange neighbours, which is consistent with the pattern we observed in this study population (Fig. 2). However, during high-density years of the 2-year cycles, most orange females will have orange neighbours, which are associated with decreased survival of females to later clutches and a dramatic collapse in the number of progeny recruited by orange females on the first clutch (Sinervo et al., 2000a). Thus, there is a tight link between orange female fitness, corticosterone and density regulation in this population.

Several mechanisms could be generating these observed morph differences in home range distribution. Agonistic behaviours of female lizards can be directed at other females during territorial disputes or dominance interactions (Stamps, 1973; Ruby, 1986; Woodley & Moore, 1999). Female aggression increases during the reproductive season in many iguanid and phyrnosomatid species and aggression is correlated with the onset of bright throat or body coloration (Ferguson, 1976; Cooper, 1983; Watkins, 1997). Our field observations suggest that orange females may defend rock areas more aggressively than yellows, and subsequently, the tendency for orange females to have a lower proportion of orange female neighbours may result from behavioural differences between morphs. Orange females may avoid overlapping with other

orange females to reduce costs of aggression that may act through lowered corticosterone; however, when they do overlap, chronic agonistic interactions lower plasma corticosterone, which appears to have negative effects on survival.

It is also possible that these spatial patterns are a result of selection rather than behavioural adjustments. In each social neighbourhood, some individuals die after the start of the breeding season but before the development of throat coloration. During 1998–99, ∼40% of female individuals died before reproduction and throat colour development. Orange females that overlap home ranges with other orange females may experience decreased survival, leading to a situation in which they are less likely to be found in close proximity to other orange females during reproduction. Likewise, the process of cryptic selection may also bias the measurement of corticosterone. The effects of cryptic selection cannot be evaluated until genetic markers that differentiate between morphs at hatching are available (Lande & Price, 1989).

The evidence presented here, in conjunction with our earlier work on immune function and fitness (Sinervo et al., 2000a; Svensson et al., 2001a,b), indicates that the two female morphs differ in the degree of phenotypic plasticity in reproduction and physiological traits. Orange females appear to be more sensitive to changes in the local social environment, especially towards neighbours of the same morphotype. In contrast, yellow females seem to be more buffered against external social factors. Reaction norms of yellow females appear to be more canalized, i.e. given temporal fluctuations in local social environments, yellows tend to produce a standard response (also see Svensson et al., 2001a,b, 2002). The results in this field study were also confirmed in a laboratory study, in which we experimentally manipulated the social environment in the form of number of yellow and orange females and evaluated corticosterone response (Comendant, 2002). Furthermore, corticosterone also seems to be involved in offspring sex allocation (Sinervo & Denardo, 1996; Comendant, 2002), underscoring its importance in adaptive plasticity of reproduction in this system.

The adaptive significance of differences in plasticity and canalization between morphs remains to be resolved (see Lively, 1986). Conceivably, if different reaction norms were favoured in relation to different social factors in morphs, selection would be acting on phenotypic plasticity. Systems with several genetic morphs coexisting within the same population provide ideal systems for further investigation of the evolutionary significance of morphotype-by-environment interactions and the adaptive nature of plasticity. Further studies on the role of corticosterone in reproductive investment to clutch size, egg size and sex ratio is the obvious next step to uncover the adaptive nature of the corticosterone response.

Acknowledgments

References

Astheimer, L.B., Buttemer, W.A. & Wingfield, J.C. 1992. Interactions of corticosterone with feeding activity and metabolism in passerine birds. *Ornis Scandinavica* **23**: 355–365.

Brandon, R.N. 1990. *Adaptation and Environment.* Princeton University Press, Princeton, NJ, USA.

Bremner, J.D. 1999. Does stress damage the brain? *Biol Psychiatry* **45**: 797–805.

Comendant, T. 2002. *Effects of Social Competition on Endocrine Function and Life-history Evolution in Female Morphs of the Side-blocked Lizard, Uta stansburiana*, PhD. University of California, Santa Cruz, CA, USA.

Cooper, W.E. 1983. Female color change in the keeled earless lizard, *Holbrookia propinqua*: relationship to the reproductive cycle. *Southwest. Nat.* **28**: 275–280.

Creel, S. 2001. Social stress and costs of dominance. *Trends Ecol. Evol.* **16**: 491–497.

Doughty, P. & Sinervo, B. 1994. The effects of habitat, time of hatching, and body size on the dispersal of hatchling *Uta stansburiana*. *J. Herpetol.* **28**: 485–490.

Ferguson, G.W. 1976. Color change and reproductive cycling in female collared lizards (*Crotaphytus collaris*). *Copeia* **3**: 491–494.

Greenberg, N. & Wingfield, J. 1987. Stress and reproduction: reciprocal relationships. In: *Hormones and Reproduction in Fishes, Amphibians, and Reptiles* (D.O. Norris & R.E. Jones eds), pp. 461–503. Plenum Press, New York.

Ingle, D.J. 1952. The role of the adrenal cortex in homeostasis. *J. Endocrinol.* **8**: xxiii–xxxvii.

Jessop, T.S., Knapp, R., Whittier, J.M. & Limpus, C.J. 2002. Dynamic endocrine responses to stress: evidence for energetic constraints and status dependence in breeding male green turtles. *Gen. Comp. Endocrinol.* **126**: 59–67.

Ketterson, E.D. & Nolan, V. 1992. Hormones and life histories: an integrative approach. *Am. Nat.* **140**: S33–S62.

Knapp, R. & Moore, M.C. 1996. Male morphs in tree lizards, *Urosaurus ornatus*, have different delayed hormonal responses to aggressive encounters. *Anim. Behav.* **52**: 1045–1055.

Knapp, R. & Moore, M.C. 1997. Male morphs in tree lizards have different testosterone responses to elevated levels of corticosterone. *Gen. Comp. Endocrinol.* **107**: 273–279.

Lande, R. & Price, T. 1989. Genetic correlations and maternal effect coefficient obtained from parent offspring regression. *Genetics* **122**: 915–922.

Lively, C.M. 1986. Canalization versus developmental conversion in a spatially variable environment. *Am. Nat.* **128**: 561–572.

Moore, M.C. & Marler, C.A. 1988. Hormones, behavior, and the environment: an evolutionary perspective. In: *Processing of Environmental Information in Vertebrates* (M.H. Stetson ed.), pp. 71–83. Springer-Verlag, New York.

Moore, M.C., Hews, D.K. & Knapp, R. 1998. Hormonal control and evolution of alternative male phenotpyes: generalizations of models for sexual differentiation. *Am. Zool.* **38**: 133–151.

Munck, A., Guyre, P. & Holbrook, N. 1994. Physiological functions of glucocorticosteroids in stress and their relation to pharmacological actions. *Endocr. Rev.* **5**: 25–44.

Ruby, D.E. 1986. Selection of home range site by females of the lizard, *Sceloporus jarrovi. J. Herpetol.* **203**: 466–469.

Sapolsky, R.M. 1987. Stress, social status, and reproductive physiology in free-living baboons. In: *Psychobiology of Reproductive Behavior: an Evolutionary Perspective* (D. Crews ed.), pp. 291–322. Prentice-Hall, Englewood Cliffs, NJ, USA.

Sapolsky, R.M. 1992. Neuroendocrinology of the stress response. In: *Behavioral Endocrinology* (J.B. Becker, S.M. Breedlove & D. Crews eds), pp. 287–324. MIT Press, Cambridge, MA, USA.

SAS Institute Inc. (1989). JMP Statistical Software 5.0. Cary, NC.

Schwabl, H. 1995. Individual variation of the acute adrenocortical response to stress in the white-throated sparrow. *Zoology* **99**: 113–130.

Sinervo, B. & Denardo, D.F. 1996. Costs of reproduction in the wild: path analysis of natural selection and experimental tests of causation. *Evolution* **50**: 1299–1313.

Sinervo, B. & Licht, P. 1991. Hormonal and physiological control of clutch size, egg size, and egg shape in side-blotched lizards (*Uta stansburiana*): constraints on the evolution of lizard life histories. *J. Exp. Zool.* **257**: 252–264.

Sinervo, B. & Svensson, E. 1998. Mechanistic and selective causes of life history trade-offs and plasticity. *Oikos* **83**: 432–442.

Sinervo, B., Svensson, E. & Comendant, T. 2000a. Density cycles and an offspring quantity and quality game driven by natural selection. *Nature* **406**: 985–988.

Sinervo, B., Miles, D.B., DeNardo, D.F. & Frankino, W.A. 2000b. Testosterone, endurance, and Darwinian fitness; natural and sexual selection on the physiological basis of alternative male behaviors in side-blotched lizards. *Horm. Behav.* **38**: 222–223.

Stamps, J. 1973. Displays and social organization in female *Anolis aeneus. Copeia* **2**: 264–272.

Svensson, E., Sinervo, B. & Comendant, T. 2001a. Condition, genotype-by-environment interaction and correlation selection in lizard life-history morphs. *Evolution* **55**: 2053–2069.

Svensson, E., Sinervo, B. & Comendant, T. 2001b. Density dependent competition and selection on immune function in genetic lizard morphs. *Proc. Natl. Acad. Sci. USA* **98**: 12 561–12 565.

Svensson, E.I., Sinervo, B. & Comendant, T. 2002. Mechanistic and experimental analysis of condition and reproduction in a polymorphic lizard. *J. Evol. Biol.* **15**: 1034–1047.

Watkins, G. 1997. Inter-sexual signalling and the functions of female coloration in the tropidurid lizard *Microlophus occipitalis. Anim. Behav.* **53**: 843–852.

West-Eberhard, M.J. 1989. Phenotypic plasticity and the origins of diversity. In: *Annual Review of Ecology and Systematics*

(R.F. Johnston ed.), vol. 20, pp. 249–278. Annual Reviews Inc., Palo Alto, CA, USA.

Wilson, B. & Wingfield, J. 1992. Correlations between female reproductive condition and plasma corticosterone in the lizard *Uta stansburiana. Copeia* **3**: 691–697.

Wingfield, J.C. & Ramenofsky, M. 1999. Hormones and the behavioral ecology of stress. In: *Stress Physiology in Animals* (P.H.M. Baum ed.), pp. 1–51. CHC Press, Sheffield, England.

Wingfield, J.C., Vleck, C.M. & Moore, M.C. 1992. Seasonal changes of the adrenocortical response to stress in birds of the sonoran desert. *J. Exp. Zool.* **264**: 419–428.

Wingfield, J.C., Breuner, C., Jacobs, J., Lynn, S., Ramenofsky, M. & Richards, R. 1998. Ecological bases of hormone-behavior interactions: the emergency life history stage. *Am. Zool.* **38**: 191–206.

Woodley, S.K. & Moore, M.C. 1999. Female territorial aggression and steroid hormones in mountain spiny lizards. *Anim. Behav.* **57**: 1083–1089.