Thesis of dissertation

INDIVIDUAL QUALITY AND MULTIPLE SIGNALLING SYSTEMS IN THE EUROPEAN GREEN LIZARD (*LACERTA VIRIDIS*)

Orsolya Rita Molnár

Department of Systematic Zoology and Ecology
Eötvös Loránd University

Supervisor:

Prof. János Török DSc.

Gábor Herczeg PhD.

PhD School of Biology

Chair: Prof. Anna Erdei DSc.

Zootaxonomy-Animal Ecology-Hidrobiology Program

Program leader: Prof. Klára Dózsa-Farkas, DSc.

BUDAPEST, 2013

Background

Sexual selection

During evolutional processes, only traits resulting in the highest individual fitness with respect to certain constraints (e.g. genetic correlations) can be fixed in a population. The higher the fitness of an individual, the larger proportion of future generations will be carrying its alleles. The two main components of fitness, (i) current reproduction and (ii) survival are in trade-off, since only a limited amount of resources is available in natural populations and the energy allocated into reproductive traits decreases that available for somatic traits and thus survival.

There are numerous species known to have conspicuous characteristics, or show behavioural displays that considerably decrease their survival (Grafen 1990, Guilford 1995). These elaborate traits can raise developmental or maintenance costs, that also decrease the owner's probability of survival. The theory of sexual selection explains how these detrimental attributes persist through evolution (Darwin 1871). In the classic approach, sexual selection is considered as a competition for a common resource, similar to natural selection, however, in this case the limited resource is the reproductive partner instead of an environmental factor. This competition results in the appearance of phenotypic traits, i.e. sexual signals that have a positive effect on the reproductive success, but not on the survival of the owner. Sexual signals can be chemical, audio, visual or behavioural traits, but all share the attributes of (i) being preferred by conspecifics of the opposite gender and (ii) being inherited by the offspring. Individuals maintaining more intense signals are more successful in mating, but experience a lower rate of survival, therefore reproduction and survival are in a trade-off (Schluter & Price 1993).

The classic approach was further developed and completed with several new theories. Andersson (1994) defines sexual selection as a process of natural selection and classifies all individual traits into one of three categories: (a) those, that favored only by other processes of natural selection, (b) those, that are favored only by sexual selection and (c) those, that are potentially favored by both types of processes. Carranza (2009) raises the idea that sexual selection leads to different adaptations in each gender and the same gene can affect fitness in diverse ways in females and males.

The intensity of selection is influenced by numerous factors that determine the speed and scale at which sexual signals develop. One important effect is *operational sex ratio* (Emlen & Oring 1977), since competition for reproductive partner increases among individuals that are in higher numbers, therefore sexual selection intensifies within the sex present in a larger proportion. Influence of operational sex ratio is strong, but not exclusive, as *potential reproductive rate*, the maximum number of offspring produced by parents within a standard time period, also has a considerable effect (Cluttonbrock & Vincent 1991).

The two main processes of sexual selection are intrasexual and intersexual selection. Males try to expel each other from reproduction prior to mating (Clutton-Brock *et al.* 1979, Ligon *et al.* 1990, Qvarnström 1997, Candolin 2005), while after mating they can increase their reproductive success by killing other males' sperm (Birkhead & Moller 1998) or offspring (Hrdy 1979) or through mate guarding (Birkhead 1979). Intersexual selection includes male (Hill 1993) or female mate choice (Censky 1997, Candolin 2003) before, and cryptic female mate choice after mating (Kokko *et al.* 2003).

Individuals can increase their own fitness if reproductive partners maximize their reproductive efforts (Emlen & Oring 1977, Andersson 1982). This can be facilitated by informing conspecifics about advantageous traits, thus making estimating owner quality easier. Wearing elaborate traits is an efficient way of signalling quality, as the preference of the opposite sex increases with intensity of the signal. Several theories explaining the evolution of these conspicuous traits have been developed. Fisher's *sexy son hypothesis* (1930) stated that females start preferring males with more elaborate traits due to a random mutation, thereby producing males with more intense signals and females preferring those, a process named *runaway selection*. This was followed by Trivers' *good gene hypothesis* (1972) that described a genetic connection between signal intensity and owner quality, hereby allowing conspecifics to estimate individual quality from signal expression. Zahavi developed the *handicap hypothesis* (1975), according to which honesty of a signal is ensured by the developmental and maintenance costs associated with it, thus only individuals of better quality can afford to express conspicuous signals. Finally, Hamilton and Zuk (Hamilton & Zuk 1982) suggest the selectional pressure of endoparasite load drives the evolution of elaborate traits. They presume that in species showing higher prevalence, better quality individuals are more resistant and are thus capable of allocating more energy into colouration. Studies supporting predictions of the latter theory have previously been performed, however, results are contradictory and the hypothesis has not been proved on reptiles.

Study species, the European green lizard (*Lacerta viridis* Laurenti, 1768)

The European green lizard is one of the largest lizard species in Hungary. It tolerates perturbance well, it is therefore found on plains, hill and mountainsides, forest sides and scrub grasslands, as well as city parks and yards. The study population was found near Tápiószentmárton, Hungary: 47°20′25″ N, 19°47′11″ E. The species shows intense sexual dimorphism and dichromatism, males are larger and more robust, and colouration is very diverse. Dorsal parts of the body and head are usually green or brown, belly colour reaches from dull white to bright yellow. During the breeding season males develop bright blue nuptial throat patch. Breeding season lasts from the end of April to mid-May, females are then gravid for approximately 40-50 days, and lay 3 to 6 eggs into a 20-30 cm deep hole and cover them with soil. Eggs hatch after 60 days and juveniles are independent hereafter.

Aims of the study

Since our previous results have shown that nuptial throat colour is a sexually selected secondary sexual trait, the aim of this study was to reveal information content of this signal, and investigate, whether it acts as a multiple signalling system. I therefore investigated:

- the connection between nuptial colour and morphological traits
- the connection between nuptial colour and spatial behaviour
- the connection between nuptial colour and health state, characterized by endoparasite load

I. The connection between nuptial colour and morphological traits

Material and methods

I collected morphological and colour variables of 66 males form three consecutive years. I measured body length, body weight, head size, level of directional asymmetry and ectoparasite load (*Ixodes* sp., Ixodidae), and recorded colour variables of throat patch with a spectrometer. Colouration was characterized by total brightness, ultraviolet (UV) chroma and blue chroma. I used General Linear Models (GLM) to reveal coherences between colour variables and other individual traits, colour variables were entered as dependent variables, other individual characteristics as independent variables, and year of capture was the categorical predictor. I used backward stepwise model selection.

Results and discussion

UV chroma and body condition showed negative correlation, which can occur due to the maintenance costs of elaborate colouration. Similar connection was found between UV colour and level of directional asymmetry, which can also be explained with the costs of intense signals raise. Since high level of directional asymmetry is advantageous for the owner, decrease of asymmetry could appear as a cost of intense sexual signals.

Total brightness was positively correlated with body and head size, which can be explained with larger individuals signalling their better quality. Since larger animals usually have better survival, owners can increase their reproductive success by signalling this advantageous trait. Additionally, head size has previously been shown to be connected to bite force, which trait positively affects intraspecific competition. Alternatively, bright colour can act as an amplifier, making estimation of head size more efficient.

All three colour variables showed significant connection with the year of capture, which can be due to colouration being strongly environment-dependent, as average yearly temperature has an important effect on throat colour.

II. The connection between nuptial colouration and spatial behaviour

Material and methods

I recorded data and home range size from 40 males during two consecutive years, together with the number of females sighed on each male's home range. Morphological and colour variables were measured as described in the previous chapter. Spatial behaviour was characterized with total number of sightings and average distance between sightings. Principal Components Analysis (PCA) was run on the two spatial variables to determine spatial strategy or random movement. Correlations between spatial strategy and individual traits were searched for with Generalized Linear Models (GLZ), and GLM were used to determine connection between individual traits and random movement. Among territorial males I further performed GLM to reveal coherences between territory size and individual traits.

Results and discussion

I showed two different space use systems in the two years, whereas males in the first year followed either territorial or floater strategies, while those in the second year appeared to move randomly. This can be explained with the difference in density and surrounding vegetation of the two populations.

In the first year, floaters had brighter throats than territorial animals, which can be due to the costs of defending a territory.

Within territorial males, those with larger areas had lower brightness and blue chroma, but larger head size. Since defending a larger territory has higher costs, the owner could have reduced colouration, and only those individuals more successful in intraspecific competition, i.e. with greater bit force and head size can afford to do so.

III. The connection between nuptial colouration and health state

Material and methods

I collected morphological and colour data and blood samples from 24 males during the breeding season. Morphological and colour variables were measured as described in the previous chapters. I made blood smears for all individuals and used them to quantify parasite prevalence for the population and infection intensity for each individual. I used GLM to search for connections between infection intensity and individual traits.

Results and discussion

Results showed that parasite prevalence was extremely high for the population.

Throat and belly colour were both negatively associated with parasite load, thus supporting predictions for species with high prevalence of the Hamilton-Zuk hypothesis, namely that resistant individuals can afford to allocate more energy into their sexual colouration. Additionally, rate of infection showed positive correlation with body size and condition, which can be explained with the immunosenescence of older males and costs of maintaining better body condition. Directional asymmetry was also positively correlated with infection intensity, which can be a cost of bearing an advantageous trait. Finally, number of ticks was negatively correlated with endoparasite load, which can be a result of the immune reaction to tick bites affecting endoparasites, as well.

New scientific results of the dissertation

(I.) I was first to show that a trait previously proven to be sexually selected acts as a multiple signalling system in reptiles.
(II.) I demonstrated condition-dependence of a trait affecting preference and competition, thus proved it to be an honest signal of quality.
(III.) I described multiple space use strategies in a reptile species referred to as territorial.
(IV.) I showed spatial strategies to be represented in sexual colour signals.
(V.) I found correlation between a multiple signalling colour variable and other colourations and endoparasite load.

(VI.) This is the first study to find results supporting predictions of the Hamilton-Zuk hypothesis in a reptile.

References

ANDERSSON, M. 1982. Sexual Selection, Natural-Selection and Quality Advertisement. *Biological Journal of the Linnean Society*, 17: 375-393.

ANDERSSON, M. 1994. *Sexual Selection*. Princeton: Princeton University Press.

BIRKHEAD, T. R. 1979. Mate guarding in the magpie Pica pica. *Animal Behaviour*, 27: 866-874.

BIRKHEAD, T. R., A. P. MOLLER. 1998. *Sperm Competition and Sexual Selection*. San Diego: Academic Press.

CANDOLIN, U. 2003. The use of multiple cues in mate choice. *Biological Reviews*, 78: 575-595.

CANDOLIN, U. 2005. Why do multiple traits determine mating success? Differential use in female choice and male competition in a water boatman. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 272: 47-52.

CARRANZA, J. 2009. Defining sexual selection as sex-dependent selection. *Animal Behaviour*, 77: 749-751.

CENSKY, E. J. 1997. Female mate choice in the non-territorial lizard Ameiva plei (Teiidae). *Behavioral Ecology and Sociobiology*, 40: 221-225.

CLUTTON-BROCK, T. H., S. D. ALBON, R. M. GIBSON, F. E. GUINNESS. 1979. The logical stag: Adaptive aspects of fighting in red deer (Cervus elaphus L.). *Animal Behaviour*, 27: 211-225.

CLUTTONBROCK, T. H., A. C. J. VINCENT. 1991. Sexual Selection and the Potential Reproductive Rates of Males and Females. *Nature*, 351: 58-60.

DARWIN, C. 1871. *The descent of man and selection in relation to sex*. London: Murray.

EMLEN, S. T., L. W. ORING. 1977. Ecology, Sexual Selection and the Evolution of Mating Systems. *Science*, 197: 215-223.

FISHER, R. A. 1930. *The Genetical Theory of Natural Selection*. Oxford: Clarendon Press.

GRAFEN, A. 1990. Biological Signals as Handicaps. *Journal of Theoretical Biology*, 144: 517-546.

GUILFORD, T. 1995. Animal Signals - All Honesty and Light. *Trends in Ecology & Evolution*, 10: 100-101.

HAMILTON, W. D., M. ZUK. 1982. Heritable True Fitness and Bright Birds - a Role for Parasites. *Science*, 218: 384-387.

HILL, G. E. 1993. Male mate choice and the evolution of female plumage coloration in the house finch. *Evolution*, 1515-1525.

HRDY, S. B. 1979. Infanticide among animals: A review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology*, 1: 13-40.

KOKKO, H., R. BROOKS, M. D. JENNIONS, J. MORLEY. 2003. The evolution of mate choice and mating biases. *Proceedings of the Royal Society B-Biological Sciences*, 270: 653-664.

LIGON, J. D., R. THORNHILL, M. ZUK, K. JOHNSON. 1990. Male-male competition, ornamentation and the role of testosterone in sexual selection in red jungle fowl. *Animal Behaviour*, 40: 367-373.

QVARNSTRÖM, A. 1997. Experimentally increased badge size increases male competition and reduces male parental care in the collared flycatcher. *Proceedings of the Royal Society B-Biological Sciences*, 264: 1225-1231.

SCHLUTER, D., T. PRICE. 1993. Honesty, Perception and Population Divergence in Sexually Selected Traits. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 253: 117-122.

TRIVERS, R. L. 1972. *Parental investment and sexual selection*. Chicago: Aldine.

ZAHAVI, A. 1975. Mate Selection - Selection for a Handicap. *Journal of Theoretical Biology*, 53: 205-214.

Publications and manuscripts

Articles included in the dissertation

- MOLNÁR, O., K. BAJER, B. MÉSZÁROS, J. TÖRÖK, G. HERCZEG. 2013 **Negative correlation between nuptial throat colour and blood parasite load in male European green lizards supports the Hamilton-Zuk hypothesis** *Naturwissenschaften* DOI: 10.1007/s00114-013-1051-4
- MOLNÁR, O., K. BAJER, J. TÖRÖK, G. HERCZEG. 2012. **Individual quality and nuptial throat colour in male European green lizards** *Journal of Zoology* 287:233-239
- MOLNÁR ,O., K. BAJER, J. TÖRÖK, G. HERCZEG. 2013. **Space use strategies and nuptial colour in the European green lizard (Lacerta viridis)** *Herpetologica* (under review)

Other publications

- BAJER, K., O. MOLNÁR, J. TÖRÖK, G. HERCZEG. 2012. **Temperature but not available energy effects the expression of a sexually selected ultraviolet (UV) colour trait in male European green lizards** *PLoS ONE* 7:e34359
- BAJER, K., O. MOLNÁR, J. TÖRÖK, G. HERCZEG. 2011. **Ultraviolet nuptial colour determines fight success in male European green lizards (*Lacerta viridis*)** *Biology Letters* 7:866-868
- BAJER, K., O. MOLNÁR, J. TÖRÖK, G. HERCZEG. 2010. **Female European green lizards (*Lacerta viridis)* prefer males with high ultraviolet throat reflectance** *Behavioral Ecology and Sociobiology* 64:2007-2014