The behavioural ecology of animal signals:

A functional theoretical perspective and its application to the study of scent marks in the lizard *Podarcis hispanica*

Pau Carazo Ferrandis

Universidad de Valencia

VNIVERSITAT DE VALÈNCIA

Facultat de Ciencias Biológicas

Instituto Cavanilles de Biodiversidad y Biología Evolutiva

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Fdo.: Pau Carazo Ferrandis

Tesis dirigida y codirigida por los doctores:

Fdo.: Enrique Font Bisier
Profesor Titular de Zoología
Universidad de Valencia

Fdo.: Ester Desfilis Barceló
Ayudante Doctora de Psicobiología
Universidad Complutense de Madrid

Fdo.: Miguel Molina Borja
Profesor Titular de Zoología
Universidad de La Laguna

"Every day you may make progress. Every step may be fruitful. Yet there will stretch out before you an ever-lengthening, ever-ascending, ever-improving path. You know you will never get to the end of the journey. But this, so far from discouraging, only adds to the joy and glory of the climb."

Winston Churchill

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Part I. General introduction

Chapter 1- Overview of ideas and main objectives

1.1 The behavioural ecology of animal signals

This PhD dissertation is all about the study of the adaptive value of animal signals. Its scope is both theoretical and empirical, as are its main objectives. This duality is reflected in its two constituent parts. The first one ('towards a functional theoretical framework of animal communication') is an exclusively theoretical analysis in which we focus on a historical problem concerning the way we conceptualize communication, and thus the way we study animal signals. Briefly, the search for a comprehensive theoretical framework in animal communication has repeatedly stumbled upon a controversy that is deeply ingrained in the study of animal communication. This controversy is about the function of animal signals. For different reasons (some historical, others probably stemming from the pervasive application of linguistic concepts and ideas) the answers and theories that have been put forward have failed to untangle what some regard as the Gordian knot in the study of animal communication. My aim is to provide new insight into this conundrum; a new perspective to the way we conceptualize animal signals, and thus to the way we define and study animal communication. I begin by conducting a brief introduction to the field of animal communication, with particular emphasis on the way animal communication has been defined and conceptualized since the advent of modern biology (chapter 2), which was marked by the publication of 'The Origin of Species' by Charles Robert Darwin (1859). I beware readers that the aim of this chapter is not to present a critical analysis or a thorough review of the state of the field, but to provide a concise introduction of its

most central concepts and general outline regarding, mostly, the function of animal signals. Note, for example, that I devote no attention whatsoever to the proximate dimension (i.e. mechanisms and development) of animal signals, and only very briefly touch upon the tactical design of animal signals (Guilford & Dawkins 1991; Bradbury & Vehrencamp 1998). The main aim of this chapter is hence to serve as a prelude to the functional analysis discussed in chapter 3.

Chapter 3 begins with a thorough review of the essentials of current notions of animal communication, and one of its aims is to provide a state of the art on the currently revived debate about the function of animal signals: do animal signals transmit information? For decades, animal signals have been portrayed as carriers of information. However, the concept of information has been plagued with ambiguities and the study of its role in communication has been systematically pervaded by ideas borrowed from human linguistics, ideas that have little to do with most, if not all, animal communication. Recent analyses have suggested that we may avoid this confusion by focusing exclusively on the effects of animal signals (i.e. their function from the perspective of senders), and have reached the conclusion that information transfer is an irrelevant or, at best, a secondary factor in the evolution of animal signals (Scott-Phillips 2008, 2009; Rendall *et al.* 2009). In this chapter, we discuss the existence of a duality in the function of animal signals (i.e. to serve both sender and receiver's interests) and explore whether this duality can be understood without the notion of information. We scrutinize the recent proposition that information is not something that is actively transmitted by senders and explore whether this justifies the conclusion that there is no information transfer in animal

communication (Rendall *et al.* 2009). Finally, we explore the possibility that a 'functional' definition of information may be established that integrates the duality of animal signal function into communication. We suggest a possible definition of information and discuss its underlying theoretical rationale and its possible advantages with respect to past propositions. Many of the ideas put forward in this analysis were already there, scattered throughout the scientific literature of the last two decades. However, I hope that the way in which we have realigned and put together these ideas may actually contribute in our path towards a more comprehensive evolutionary framework of animal communication.

1.2. The function of scent marks in *Podarcis hispanica*

The second part of this thesis follows the theoretical framework laid down in the first part, and is a mostly empirical investigation into the function of scent marks in the Iberian wall lizard (*Podarcis hispanica sensu lato*, hereafter *Podarcis hispanica*; see chapter 4). In particular, it addresses the types of functional information that may be extracted by receivers from scent marks. Scent marks are chemicals deliberately (i.e. evolved to be) placed in the environment, and are among the most ubiquitous social signals in terrestrial vertebrates (Wyatt 2003; Müller-Schwarze 2006). Singular in that they are usually perceived in the absence of signallers, the study of scent mark function has received considerably less attention than they deserve given their ubiquity (Gosling & Roberts 2001; Wyatt 2003). For decades, scent marks have been depicted as 'no trespass' signals, as mere chemical sign posts for intruders. Recent studies, however, are unveiling a much more complex picture in which scent marks may be used to asses diverse aspects of a male's quality as a rival or as a prospective mate, or

about the quality of its territory. One peculiarity of scent marks is that, apart from their intrinsic properties (i.e. derived from their chemical composition), extrinsic characteristics such as their spatial location within a territory (or in relation to other male's scent marks) or their freshness may be used by receivers to extract information much more complex and subtle than previously suspected. Unfortunately, our understanding of the functional value of scent marks is still in its infancy. Lacertid lizards in general, and *Podarcis hispanica* lizards in particular, represent an ideal study group to address this aim. They possess well-developed chemosensory abilities and are territorial lizards that exhibit frequent and intense male-male agonistic encounters and a resource-based polygynandrous mating system where, from a strictly theoretical point of view, scent marks are predicted to be particularly important (Gosling & Roberts 2001; see also introduction to chapter 5). My fundamental aim when studying lizard scent marks has been to try to disentangle not only the kind of information that scent marks may convey to receivers, but its evolutionary function to senders and receivers. In order to do so, we have made a special effort to design a series of experimental setups with functional significance given the questions raised, and the biology and behaviour of the species involved (i.e. *Podarcis hispanica*).

Chapter 4 is an introduction to the study of scent marks in lizards. In it, I outline important details of the biology and taxonomic status of *P. hispanica*, as well as some background generalities about the social behaviour and chemical communication of lacertid lizards. I also sketch the controversy on the taxonomy of the genus *Podarcis.* My intention here is to clarify any possible misunderstandings in relation to the specific status of

the individuals in my study population, apparently included in the *P. hispanica* species complex (Carretero 2008; Renoult *et al.* 2009). Available evidence suggests that the individuals in my study population (around the city of Valencia) may pertain to the *Podarcis liolepis* evolutionary lineage from the East Mediterranean coast of the Iberian Peninsula. However, the still unresolved nature of its taxonomy advised us to err on the side of caution and maintain its classic denomination of *Podarcis hispanica*. As already stated, chapter 4 also introduces the study of chemical communication in lizards. The overriding importance of chemical communication in squamates (i.e. lizards and snakes) is evident in the existence of three well-developed systems for the detection and processing of chemical stimuli. I describe these sensory systems and their relative importance for the detection of socially relevant signals along with the mechanisms responsible for the production of scent marks in lizards. Finally, I also present a brief review of the social behaviours most typically found in lizards, with special emphasis on territorial species such as most *Podarcis*.

Chapters 5 and 6 describe two series of experiments investigating the function of scent marks as social signals mediating male-male sexual competition and territorial behaviour. Several studies have addressed the chemosensory ability of lizards to discriminate among different chemical cues in relation to the specific identity, sexual status, and reproductive quality and condition of its bearer (Simon 1983; Mason 1992; Halpern 1992; Gómez *et al.* 1993; Schwenk 1993, 1995; Font 1996; Font & Desfilis 2002; Wyatt 2003; Pianka & Vitt 2003; López & Martín 2004). However, functional approaches to the study of scent marks and other chemical stimuli are

much scarcer. Demonstrating that an animal is capable of detecting a difference between two stimuli does not imply that such stimuli are biologically relevant, and provides little or no insight into the related fitness benefits to senders and receivers. Without this knowledge, it is difficult to draw a conclusion about the evolution and function of chemical social signals in lizards. Thus, the question about the kind of information that may be contained in certain stimuli is only a first step to understanding social signals. How do receivers use (i.e. respond to) that information? Are receiver responses always adaptive for senders? What are the costs and benefits of producing and responding to certain signals? In other words, why are signals adaptive for senders and receivers? These, as argued in chapter 3, are the key questions that must be answered in order to understand any given communicative system.

Modern ideas about the function of scent marks in territorial species stress their role as social signals potentially mediating competitor assessment. According to this view, scent marks not only signal resident status and/or act as chemical 'keep out' barriers to intruders (traditional hypothesis), but may be used by receivers to derive information about the costs of exploiting a given area. However, few studies have directly addressed this hypothesis and its specific predictions. In chapter 5, I describe an experiment setup to simulate the situation faced by an intruding male when entering the scent marked territories of rival males of varying competitive ability to test: a) whether lizards may use scent marks to derive information about the competitive ability of territory-holding lizards, b) whether scent marks function as chemical barriers or, on the contrary, whether receivers base their decision to explore scent marked

areas on the information they may contain about the sender, and c) whether receiver response is sensitive to seasonal changes in the cost to benefit balance of entering areas scent marked by territory-holding males.

If chapter 5 examines the function of scent marks from the perspective of a male intruding in another male's territory, chapter 6 looks at the problem from the point of view of territory holding males. Namely, in this chapter I address how territory holding males may use scent marks available in the environment to their own advantage: why are scent marks adaptive for territory-holding males? Previous studies have already suggested that scent marks may aid territorial males in their combat against other rivals because they allow intruders to identify them as the resident (e.g. by 'scent matching'; Gosling & Roberts 2001). However, in a territorial system where males build their territories around valuable resources, the greatest threat to territory-holding males are likely other territory-holding neighbour males whose competitive ability is also likely to be high. Lizards studies have traditionally stressed the advantages of rival discrimination (i.e. 'dear enemy' recognition) in those species that actively defend their territories against the repeated intrusions of rival males, whereby both the energetic costs of territory defence and the risks of suffering injuries can be minimized by reducing aggression towards familiar neighbours (e.g. Stamps & Krishnan 1998; Whiting 1999; López & Martín 2001, 2002). However, although the assumption that the relative threat posed by a rival is proportional to its degree of familiarity is likely to hold in many species (Temeles 1994), the idea that potential threat and familiarity are related overlooks some instances where it may not hold (e.g. Müller & Manser 2007). For example, the threat posed by different familiar rivals is bound to

vary, regardless of familiarity, according to their competitive potential (which may, and in most cases will, vary with time) or to the degree of territory overlap with the owner (Switzer *et al.* 2001). Therefore, the ability to recognize other lizards according to their familiarity will not suffice in a complex territorial system where the threat posed by territorial neighbours and/or floater males fluctuates according to a series of inter-related factors, such as lizard age, body condition (e.g. injuries, nutritional status), or available resources (e.g. receptive females present in the territory at any given time). Consequently, evolution should favour males capable of recognizing individual rivals, and allocate their efforts against territorial intrusions according to the specific threat posed by each rival at any given time. In this chapter, we describe an experiment designed to address the existence of individual recognition in *P. hispanica*, and to study its consequences for our understanding of territorial systems in lizards. To this end, we designed a modification of a typical habituation-dishabituation procedure. The specific aims of this investigation were twofold. Knowledge about the distribution and functional significance of individual recognition (i.e. 'true individual recognition' see chapter 6) is sparse, or non-existent, in many vertebrate groups (e.g. reptiles). A specific aim was to investigate the existence of individual recognition in a lizard were it would seem to be evolutionary advantageous. Incidentally, this would be the first evidence of true individual recognition in a territorial lizard (in reptiles, true individual recognition has only been previously reported in geckos in the context of mate choice; LaDage & Ferkin 2006). Second, I wanted to examine the functional role of true individual recognition, and its consequences for territorial behaviour in *P. hispanica*, and for the way we conceptualize lizard territorial systems in general. In order to do so, we conceived an

experimental design based on the situation faced by a territory-holding male that repeatedly encounters scent marks from two neighbour males representing different threat levels (chapter 6).

True individual recognition will usually require the assessment of multiple stimuli, and its underlying mechanisms are thus bound to be more complex and sophisticated than those mediating social recognition (Thom & Hurst 2004). Moreover, it is often difficult to distinguish between discrimination based on general class features of the signals or cues involved in a given discrimination task (e.g. differences in familiarity) as opposed to specific identity features (Thom & Hurst 2004). In consequence, true individual recognition has proven notoriously elusive to empirical demonstration in most animal groups (Halpin 1986; Wyatt 2003; D'Etorre & Heinze 2005; Brennan & Kendrick 2006). A tangential benefit and subsidiary aim of this research was thus to provide a new functional paradigm, adapted from typical habituation/dishabituation protocols and correct-incorrect playback studies in birds, which may contribute to future studies of individual recognition and social behaviours in lizards.

Finally, chapters 7 and 8 are devoted to studying the role of scent marks as signals that may mediate intersexual selection in lizards. The existence of female mate choice in lizards is ripe with controversy, and female choice has seldom been recorded despite numerous investigations into lizard mating systems (Olsson & Madsen 1995, 1998; Tokarz 1995). Over the last few years, a diversity of studies have argued pro and against the existence of female mate choice in different lizard species, and new hypothesis have been put forward to explain why there is apparently good

evidence of female mate choice in some lizards, while it is seemingly absent or of little importance in many others (e.g. Sullivan & Kwiatkowski 2007). In response to this surge of new evidence, I have started chapter 7 by conducting a critical review of the new evidence for the existence of female mate choice in lizards, and to the discussion of past and current hypotheses. I discuss the possibility that females may be attending to multivariate assessment strategies that are only revealed by mate choice studies looking at multiple male traits (Hamilton & Sullivan 2005). At least in some cases, studies designed to identify the role of individual male traits may erroneously conclude that no male traits are unimportant when in fact multiple male traits are important to females. A complementary explanation for the absence of female choice involves the existence of male alternative reproductive strategies in which dominant territorial males simply clasp females and copulate with them without prior courtship, as happens in some *Anolis* and *Podarcis* lizards (Edsman 1990; Pianka & Vitt 2003; Carazo, P. & Font, E. unpublished data). In this context, females may actually have mate preferences, but they will simply not be expressed. Finally, I follow the propositions by Tokarz (1995) and Olsson & Madsen (1995) and analyse modern evidence of female mate choice with respect to the general costs of female mate choice in lizards, and to those associated with female assessment of prospective partners in particular. The costs underlying male sampling (i.e. visiting different males) and assessment (i.e. male harassment) are bound to be much larger in lizards than in other vertebrates (e.g. birds), especially in resource-based territorial species where male territories are much larger than female territories. Furthermore, the time and energy costs of assessing males will vary significantly, both among and within species, according to the socio-

ecological conditions (e.g. male density; Kwiatowski & Sullivan 2002). By factoring in all these views in an integrated analysis, my aim is to reappraise the available evidence in an effort to organize and clarify the status of this issue, and to identify fruitful paths for future research.

Chapter 8 is an investigation into the potential role of scent marks as quality signals mediating female mate choice in *Podarcis hispanica*. There seems to be some evidence of chemically mediated female mate choice in a few lacertid lizards, some closely related to *Podarcis hispanica* (Martín & López 2000, 2006a; López *et al.* 2002, 2003; Cooper & Pérez-Mellado 2002; López *et al.* 2004; López & Martín 2005). However, most of these studies have used empirical approaches that have little to do with the natural conditions under which females may actually exert mate choice in their natural habitat. We designed a mate choice experimental setup using a large naturalized chamber designed to mimic field conditions. We simulated the situation faced by a *Podarcis hispanica* female when establishing its territory in the presence of three areas of equal size: a) an area scent marked by a large male, b) an area scent marked by a small male, and c) an unscented area. Male size is not only an important determinant of male competitive ability in lizards, but it has been related to mating success in several lizard species (e.g. Wikelski & Trillmich 1997; Abell 1998; LeBas 2001).

Finally, I devote chapter 9 to a summary of the results obtained in relation to each of the specific aims of this project (see above), and to their integration in a general discussion. In chapter 10 I outline the general conclusions and contributions of this PhD thesis to our knowledge about

the function of scent marks in lizards, and to the study of animal signals at large.