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LETTER TO THE EDITOR

Cautionary comments on the influence of chemical-based interactions as potential drivers of sexual speciation in *Liolaemus* lizards

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The evolution of animal social dynamics and the origin of species through such interactions mediated by sexual selection (i.e. sexual speciation) are major challenges in current evolutionary biology, and have therefore been the subject of intense debate. Given the evolutionary significance of these problems, major efforts to assess the reliability of the evidence have been made, with controversy standing firmly (Coyne & Orr, 2004; Ritchie, 2007; Kraaijeveld, Kraaijeveld-Smit & Maan, 2011). In a recent paper, Labra (2011) suggested that the remarkable diversity of the lizard genus *Liolaemus* (220+ species) may be the result of speciation driven by chemical-based sexual selection.

The problem of selection-driven speciation is particularly interesting in a model system like *Liolaemus*, as these lizards have achieved one of the most outstanding species diversities known for a single living vertebrate genus (Pincheira-Donoso, Scolaro & Sura, 2008*c*), which is mirrored by a remarkable ecological diversity (Schulte *et al*., 2004; Pincheira-Donoso *et al*., 2009) importantly caused by radiations across a substantial range of thermal and climatic conditions (Harmon *et al*., 2003; Espinoza, Wiens & Tracy, 2004; Pincheira-Donoso, Hodgson & Tregenza, 2008*b*). Therefore, understanding the factors underlying such an extraordinary diversity can provide valuable insights into the evolutionary dynamics of active speciation rates taking place within prominent adaptive radiations. In her study, based on experimental observations of three *Liolaemus* species, Labra (2011) presents evidence suggesting that these lizards respond more actively to conspecific than to heterospecific scents secreted by male precloacal glands. This evidence reveals that focal species exhibit more exploratory responses when confronted with conspecific chemical cues. Overall, these observations provide *preliminary* clues on the functional significance of signals emitted by non-quantitative traits and their potential importance for intraspecific interactions. Based on these observations, Labra (2011) speculates about the possible effects of chemical interactions as drivers of sexual speciation in these lizards, and then concludes that these chemical-based interactions may explain the remarkable speciation rates of *Liolaemus* in general. On their own, these statements sound exciting. However, Labra's conclusions seem to suffer from two main limitations: one primarily observational, and one primarily theoretical, which I regard as conceptually more important.

Firstly, Labra reaches her conclusion of sexual speciation in *Liolaemus* lizards by stating that rapid evolution of traits involved in mating can prevent (or replace) evolution of other traits, such as morphological traits, as suggested by previous evidence observed in other organisms. She suggests that a similar scenario may explain the high speciation rates of *Liolaemus*, given that their 'relative lack of variation' in morphology and ecology may be the consequence of the rapid evolution of chemical communication systems in these lizards. However, this is a questionable statement that may result from her use of a very limited literature (she only cites Jaksic, Núñez & Ojeda, 1980; Mella, 2005) only involving a minor proportion of *Liolaemus* biodiversity restricted to central Chile. In contrast, broader-scale (in phylogeny, ecology and distribution) studies have consistently shown that these lizards have evolved substantial morphological and ecological diversity, expressed as large variation in body size, body shape, sexual dimorphism, use of microhabitats and of thermal environments, diets, life histories and dispersal potential (Cei, 1986, 1993; Harmon *et al*., 2003; Espinoza *et al*., 2004; Schulte *et al*., 2004; Cruz *et al*., 2005; Pincheira-Donoso *et al*., 2007, 2008*b*, 2009; Pincheira-Donoso, 2011; Pincheira-Donoso & Tregenza, 2011). Therefore, regardless of whether chemical systems of communication have or have not rapidly evolved in *Liolaemus*, it is difficult to support the view that the evolution of these chemical traits have prevented or limited the evolution of morphological and ecological diversity in these lizards. Indeed, while abundant evidence involving a high number of *Liolaemus* species show that ecological and morphological diversity have evolved, only a few studies restricted to a few species have shown the extent of variation in chemical communication. Also, the only study investigating the extent of evolutionary lability of the precloacal glands that produce these scents in *Liolaemus* revealed a strong effect of phylogenetic history (Pincheira-Donoso, Hodgson & Tregenza, 2008*a*).

Theoretically, Labra's paper seems to suffer from some conceptual connections between her observations and the phenomenon of evolution of reproductive isolation by divergent sexual selection. It can broadly be agreed that Labra's data may reasonably indicate that chemical signals might contribute to social interactions involved in the search or competition for mates within *Liolaemus* species, and hence, that these signals may be under sexual selection. Indeed, the coevolution between chemical scents and conspecific behavioural responses to them has often been linked to different forms of mate competition, including both male–male competition (e.g. Cooper & Vitt, 1987; Andersson, 1994) and female choice (e.g. Andersson, 1994; López, Aragon & Martin, 2003; Johansson & Jones, 2007). However, a major limitation of Labra's study is that it does not really provide any insights into the specific role of these scents in sexual selection, or more strictly speaking, whether and how their variation actually results in (or can be linked to) differential fitness between emitters mediated by their access to mates. Indeed, it is difficult to ascertain whether her results actually demonstrate species (and potentially mate) recognition rather than species discrimination. Therefore, from her analyses, it is not possible to determine which mechanism of sexual selection operates on the variation of these signals, and hence, whether these scents play a role in male contests, female choice or in both simultaneously. Despite Labra's claims that sexual speciation can result from both male contests or female choice, for sexual selection to drive the evolution of reproductive isolation, there has to be mate choice involved. Sexual speciation occurs when coevolution between preferences in one sex for sexual traits in the other proceeds in different directions between conspecific populations to create linkage disequilibrium through the rise of assortative mating that ultimately establishes reproductive barriers through prezygotic isolation between them (Panhuis *et al.*, 2001; Bolnick & Fitzpatrick, 2007). For example, experimental evidence shows that in species where female choosiness is relaxed (i.e. increased polyandry), the rate of heterospecific crossings increases (Veen *et al.*, 2011). Therefore, in the absence of evidence showing (or even suggesting) that female choice exists, or that this form of choice depends on chemical communication, it is not really possible to conclude that sexual selection is the driving force of speciation. Consequently, Labra's study does not present evidence to support the primary theoretical expectation of sexual speciation.

The limitations with Labra's three-species experiment mentioned earlier therefore make it clear that her subsequently expanded conclusions that divergent sexual selection through chemical communication may be the basis for the high speciation rates within the *Liolaemus* genus, as a whole, are unsupported and should be treated cautiously. Collectively, the problem of sexual selection-driven speciation is theoretically and empirically complex, and much debate has arisen as a result of conflicting evidence (Arnegard & Kondrashov, 2004; Coyne & Orr, 2004; Bolnick & Fitzpatrick, 2007; Ritchie, 2007; Kraaijeveld *et al.*, 2011). For this reason, any attempt to investigate the extent to which sexual selection drives the evolution of reproductive isolation should be based on stringent analyses based either on large comparative data including comprehensive species samplings and phylogenies, or on replicated species-focused experiments aiming to infer specific signals of the sexual selection dynamics that operate on populations, and hence, on their potential role in driving divergence (e.g. Tregenza, 2002; Kraaijeveld *et al.*, 2011). Labra's study lacks these two fundamental requirements, making it difficult to draw conclusions on whether sexual selection has been implicated in the origin of any of the three studied species, and virtually impossible to support the view that the active speciation events that characterize the evolutionary history of *Liolaemus* is due to chemical-based divergent sexual selection. Therefore, the question remains open, and I argue that no evidence is available yet to suggest that *Liolaemus* speciation has been influenced by sexual selection. However, Labra's efforts to address fundamental questions on the communication of these lizards should be applauded, and her research will undoubtedly prove essential to establishing the basis for the extraordinary radiation in this genus, but at present, we are some way from reaching firm conclusions on the driving forces for speciation in this group.

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