Forum

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Disentangling the complexities of vertebrate sex allocation: a role for squamate reptiles?

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Sex allocation is an important field in evolutionary biology, both historically and currently. However, while sex allocation theory has successfully predicted sex ratio bias in some taxa, most notably parasitic wasps, vertebrates are notorious for their poor fit to theoretical models. We argue that this arises from the use of very complex model systems to test relatively simple theoretical models. We further argue that squamate reptiles – lizards and snakes – have unduly been neglected in sex allocation studies and in fact may conform more readily to the underlying assumptions of existing theoretical models than many other vertebrates. We provide a five-point argument in favor of the use of squamates as model systems in sex allocation based on their diversity in sex determining mechanisms, life history biology, and ease of experimental manipulations.

The evolution of sex allocation is perhaps among the historically most important areas of evolutionary biology. Since Darwin's famous rephrasing of the problem between the first and second edition of 'The descent of man and selection in relation to sex' (Edwards 1998), sex allocation has intrigued both theoretical and empirical researchers. However, opinions on the state of the field differ. Sex allocation has been hailed by some as the greatest success story in evolutionary biology (Godfray and Werren 1996, West and Herre 2002, Seger and Stubblefield 2002), others suggest that the field is in a state of confusion (Krackow 1999, 2002, Cockburn et al. 2002). Largely, this difference stems from conflicting results from studies of different model systems. Many invertebrates, most notably parasitic hymenopterans, show strong concordance with sex allocation models (Godfray and Werren 1996, Herre et al. 2001). In contrast, the fit of vertebrate sex allocation to theoretical models is notoriously poor, both with respect to the direction and the magnitude of the adjustment (Cockburn et al. 2002, Komdeur and Pen 2002, Ewen et al. 2004).

In principle, differential sex allocation can be accomplished via two main (but not mutually exclusive) routes: (1) adjusting the sex ratio of the offspring (changing the relative numbers of males and females); (2) adjusting the investment per offspring in a sex-specific manner. While the first type of sex allocation is often straightforward to measure by simply counting the numbers of males and females, the second can pose significant logistical difficulties. Consequently, both historically and currently, researchers mainly deal with sex ratio adjustment, which may or may not be an appropriate level of analysis. The main reasons why sex allocation theory has been applied successfully to insects and not vertebrates is that, at least in some insects, parents have cheap mechanisms to adjust the sex ratio (e.g. haplodiploidy; Herre et al. 2001), the investment per offspring is either not sex-specific or relatively simple to estimate by measuring egg size, and that sex-specific fitness returns are well-documented in several cases (such as under local mate competition, Hamilton 1967). The problem with the focus on birds and mammals in vertebrate studies is that they have a very limited number of sex determining mechanisms (Krackow 1995), so it is difficult to address the extent to which sex determination constrains differential sex allocation. Secondly, the patterns of investment or parental care in birds and mammals occur at several levels, (e.g. pre- and postnatal investment of energy) and by one or both parent, with potential conflicting selection pressures (i.e. intergenomic conflict) on offspring and their parents and between male and female parents (Komdeur and Pen 2002, Parker et al. 2002, Pen 2006). This severely compromises the ability to make a priori predictions and to assess sex-specific fitness returns for a given level of investment. A model system that puts the experimenter in empirical control of all (or most) of the parameters in the theoretical models (sex determination and sex ratio adjustment, sex specific resource allocation, analysis of sex-specific fitness returns) would obviously offer highly significant opportunities for further understanding the evolution of sex allocation patterns and may bridge the gap between studies on invertebrates and vertebrates. In the present forum, we argue that many squamate reptiles (snakes and lizards) could provide such outstanding model systems and discuss the potential for future development of sex allocation studies using squamates. In doing so, we do not wish to imply that some species deserve more study than others, but rather that some valuable models for sex allocation are still left ready for exploitation and that opportunities for collaborative work across taxonomic borders may provide an important step forward in vertebrate sex allocation studies.

How do squamate reptiles offer a way forward?

Reptilian sex allocation has so far not received much attention, most evidently shown by the complete lack of treatment in a recent multi-authored book on sex ratios (Hardy 2002), and by the fact that reviews in vertebrates have exclusively dealt with mammals and birds (Frank 1990, Cockburn et al. 2002, Komdeur and Pen 2002, Krackow 2002, West and Sheldon 2002, Komdeur 2004, Sheldon and West 2005). This was not an omission by editors or authors – it accurately reflected the state of studies of reptilian sex allocation (sex allocation studies on reptiles comprise less than 6% of total studies conducted on vertebrates in the last 10 years; Fig. 1). However, squamate reptiles offer a suite of advantages (outlined below) that make them a potentially excellent model system that may provide novel insights into sex allocation biology as evident by recent publications (Uller et al. 2004, Wapstra et al. 2004, Langkilde and Shine 2005, Olsson et al. 2005a, 2005b, Le Galliard et al. 2005, Warner and Shine 2005, 2007, Allsop et al. 2006, Uller and Olsson 2006, Uller et al. 2006, Warner et al. 2007). Here we provide a five-point argument for why biologists that typically use squamate models should consider sex allocation as a field of interest and why biologists with an interest in sex allocation could benefit from considering squamate reptiles as an alternative model system.

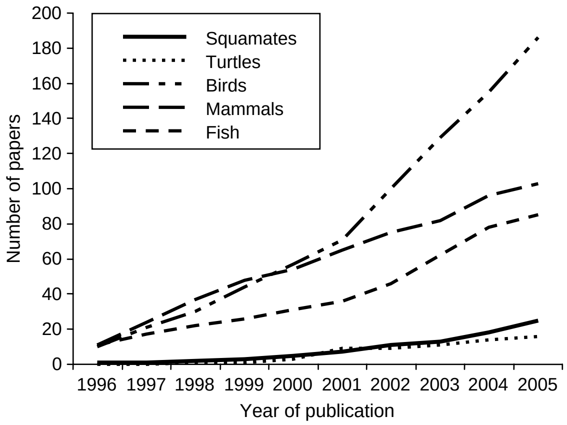

Fig. 1. Cumulative number of published papers dealing with sex allocation in different taxa from the last 10 years (1996–2005). The numbers are based on searches in the Institute for Scientific Information (ISI Web of Science) for articles referring to sex allocation or sex ratio. Abstracts were scanned to assess whether the study contained a discussion of the evolution of sex allocation or sex ratio adjustment to remove, for example, studies only focussed on proximate mechanisms of sex determination. The search only yielded one study of sex allocation in frogs (Sakisaka et al. 2000) and two in crocodilians (Girondot and Pieau 1996, Lance et al. 2000) and those taxa are therefore excluded from the figure.

Squamates possess a wide array of sex determining mechanisms

Facultative sex ratio adjustment implies that females can control the sex of their offspring. While evidence is now accumulating that this is possible in at least some reptiles, birds and mammals (Komdeur et al. 1997, 2002, Sheldon and West 2002, West and Sheldon 2004, West et al. 2005), one of the remaining challenges is to explain how variation in sex determining mechanisms impacts on the potential for sex ratio control (for example see Krackow 1999, 2002 for discussion of the constraints imposed by meiotic division). Furthermore, theoretical models suggest that selection on sex allocation can lead to evolutionary shifts in sex determination (Bull 1983, Werren et al. 2002, Kozielska et al. 2006, reviewed by Uller et al. in press a). Consequently, sex allocation and sex determination are closely linked and future progress in both fields should benefit from the use of model systems where these links can be explored.

While reptiles have thus far been largely ignored in sex allocation biology, they have in contrast been well studied with respect to sex determining mechanism (Shine 1999, Sarre et al. 2004, Janzen and Phillips 2006) largely because of the wide array of sex determining mechanisms that occurs within the group and their evolutionary lability. In lizards, even closely related taxa can differ in mode of sex determination (such as genetic sex determination without heterogamety, male or female heterogamety or temperature-dependent sex determination; Kraak and Pen 2002, Harlow 2004). Thus, how sex determining mechanisms may constrain or otherwise affect sex ratio adjustment (e.g. due to sex-specific genetic effects coupled to sex chromosomes, Olsson et al. 2004, 2005a) can be tested from meta-analytical and comparative perspectives once such data become available (Mayhew and Pen 2002, West et al. 2005). The presence of temperature-dependent sex allocation patterns in some squamates further provides a possibility to experimentally test adaptive scenarios of sex allocation and its role in the evolution of sex determination. Importantly, the supposed dichotomy (Bull 1983) between genotypic sex determination (GSD) and environmental sex determination (ESD) is now regarded as oversimplified (Sarre et al. 2004) and we doubt that rigid classificatory schemes for reptilian sex determination (as proposed by Valenzuela et al. 2003) are likely to stand the test of time. Already, recent work is revealing that temperature-dependent sex determination (TSD) and GSD can co-occur within single populations (Shine et al. 2002; see also the work by Conover and colleagues on a species of fish, the Atlantic silverside, *Menidia menidia*; Conover 2004). Hence, although extensive studies on turtles and crocodilians (taxa that are related only distantly to squamate "reptiles") suggest a general conservatism in sex-determining systems (e.g. TSD is associated with a lack of heteromorphic sex chromosomes, and generally involves steep thermal thresholds for sex determination; Ewert et al. 2004). TSD in lizards appears to be more evolutionarily labile and diverse (Robert and Thompson 2001, Shine et al. 2002, Wapstra et al. 2004, Janzen and Phillips 2006). Extensive studies on invertebrates have revealed similarly complex mosaic sex-determining systems, linked to environmental conditions and thus, presumably, selective forces (reviewed by Bull 1983, Kozielska et al. 2006). Encouragingly, mathematical models of the evolution of sex-determination predict that such complex and multifactorial systems may be stable through time under many circumstances (Kozielska et al. 2006), although more work is needed to identify the conditions that allow the persistence of mixed systems (Uller et al. in press a).

Simple patterns of parental investment

All models of sex allocation demand detailed knowledge of parental investment (Fisher 1930, Charnov 1982, Pen and Weissing 2002) which has proven to be one of the major hurdles for understanding vertebrate systems (Cockburn et al. 2002, Komdeur and Pen 2002, Komdeur 2004). For example, sex-specific allocation in birds may be achieved by adjusting offspring sex within or between clutches, egg size, onset of incubation, and post-hatching feeding rate and food quality. Clearly, the multitude of levels of investment may allow avian parents extensive adaptive control over sex allocation (Badyaev et al. 2002), but it also severely compromises the potential to make a priori predictions regarding the direction and magnitude of sex allocation at a given level of investment. Similarly in mammals, sex-specific investment can occur at several developmental stages including pre-birth and certainly via sex-specific maternal provisioning post birth (Hewison and Gaillard 1999). In contrast, energetic investment is relatively straightforward in the vast majority of squamate reptiles. Males provide no investment beyond sperm/genes at conception while female investment ends at oviposition/parturition and offspring are immediately independent (for rare exceptions see Somma 2003). Thus, interactions and conflicts between maternal and paternal investment decisions are unlikely to confound our estimates of sex allocation. As a result, by simply measuring the size of offspring at birth, maternal sex-specific allocation can be easily established, either in terms of shifts in offspring sex (Wapstra et al. 2004, Uller et al. 2006) or sex-specific offspring investment (Uller and Olsson 2006) or both (Olsson and Shine 2001, Uller and Olsson 2006). Furthermore, the evolutionary outcome of resource allocation is sensitive to conflicts between parents and offspring and among offspring (Pen and Weissing 2002, Uller 2003). For example, sex differences in competitive ability during food provisioning may be important, and sometimes confounding, selective forces on sex allocation in birds and mammals (Uller 2006). In contrast, such sex-specific sibling interactions are restricted to the prenatal stage in reptiles (Uller and Olsson 2003a, Uller et al. 2004) and to local mate competition in geographically structured populations (Madsen and Shine 1992), suggesting a greater applicability of traditional sex allocation models to squamate systems.

Most squamates are easy to sex at birth

It is ironic that most vertebrate studies of sex allocation are on a taxon where assigning offspring sex by visual inspection is virtually impossible (birds; Fig. 1). However, with the development of molecular markers in the late 90s (Griffith et al. 1998, Sheldon 1998), examination of sex allocation patterns in birds became feasible, which was followed by a significant increase in the number of published studies since 2000 (Fig. 1). In many reptiles, however, sex determination of hatchlings is relatively simple (and free of laboratory induced delays and costs), using presence (male) or absence (female) of hemipenes as a criterion (Harlow 1996). While this straightforward technique is now in common usage in at least some research groups (Olsson and Shine 2001, Robert and Thompson 2001, Shine et al. 2002, Wapstra et al. 2004, Olsson et al. 2005b, Warner and Shine 2005, 2007, Uller and Olsson 2006) two issues arise. (1) Not all species show sex differences in hemipene morphology at hatching or birth. For example, both male and female skinks of the viviparous genus *Egernia* exhibit hemipenes at hatching (Chapple 2003, While and Wapstra, unpubl.) and in monitor lizards (Varanidae) this similarity may remain throughout life (Böhme 1995). (2) Manipulation of prenatal hormone exposure can lead to retention of hemipenes in females (Panigel 1956, Uller and Olsson 2003b). These problems are however easily overcome by confirming sex in an unbiased sub-sample of offspring either histologically (Robert and Thompson 2001) or by re-sexing individuals at a later age (Uller and Olsson 2003b, Uller et al. 2006). Interestingly, the ease at which neonates can be sexed has been published for almost ten years (Harlow 1996) but it is only recently that this technique has been used to address sex allocation decisions. Given its simplicity (and speed), sex determination of hatchlings has perhaps been under-utilised when measuring offspring in many studies.

Phenotypic engineering of offspring can be straightforward

To provide strong evidence for adaptive sex allocation, we need to move from correlative studies to experimental approaches (Komdeur and Pen 2002). The majority of published avian sex ratio studies to date is correlative (e.g. only 7 out of 40 studies used in the meta-analysis by Ewen et al. (2004) were experimental; see also Komdeur and Pen 2002, Cassey et al. 2006), and the inclusion of correlative studies giving post hoc adaptive explanations is likely to lead to type 1 statistical errors, publication bias, and complications in the application of meta-analysis (Palmer 2000, Gurevitch et al. 2001, West and Sheldon 2002, Ewen et al. 2004). To gain further insight into sex ratio variation, experimental studies that test clear a priori predictions concerning causal relationships between sex ratio and the variables under investigation are needed.

In particular, it is necessary to be able to manipulate traits or circumstances that generate sex-specific fitness returns, such as female phenotype (e.g. body condition), female environment (e.g. male body condition, male ornamentation, climatic conditions) and female investment (e.g. egg size). This is perhaps where squamate reptiles offer the largest scope for progress. Many lizards are easy to keep in the laboratory or in semi-natural enclosures in relatively large numbers, which makes rigorous controlled experiments possible. For example, manipulation of basking conditions or maternal stress levels is readily conducted in the laboratory and has recently been used to investigate shifts in sex allocation patterns (Wapstra et al. 2004, Uller et al. 2005, Le Galliard et al. 2006). Furthermore, maternal resource investment can itself be manipulated using phenotypic (e.g. allocation of hormones to eggs following methods developed for birds, Groothuis and von Engelhard 2005, Uller et al. in press b) and allometric engineering (i.e. manipulation of egg size, Sinervo 1990, Sinervo et al. 1992). In contrast to birds, reptilian eggs respond well to removal of large quantities of yolk (up to 50% of original mass; Sinervo et al. 1992; see also Olsson et al. 2002 for application of these techniques to viviparous species). Although allometric engineering of offspring in lizards has revolutionized the testing of life history theory, particularly optimum offspring size (Sinervo et al. 1992, Olsson et al. 2002, Warner and Andrews 2002) it has not yet been recognised as a means of testing predictions from sex allocation theory. Specifically, it will allow tests of how sex-specific energetic allocation (size of sons vs daughters) versus offspring sex adjustment (sex ratio shifts) relates to parental and offspring fitness, without confounding effects due to parental compensation at later life stages.

Suitable for experimental field work ("real" tests)

Ultimately, understanding the evolution of sex allocation requires tests of adaptive hypotheses under natural (preferably) field conditions. This has again proven a major obstacle in many bird and mammal systems because it is often difficult to assess long-term fitness of offspring (Cockburn et al. 2002, Komdeur and Pen 2002). This problem arises through several factors including the fact that many species are relatively long-lived and that offspring frequently disperse outside the study area or population. Although some squamates share these problems, others do not. Many lizards and snakes are relatively conspicuous animals with restricted dispersal and territoriality (and geographically small home ranges, often < 100 m^2) and can therefore be marked and monitored under field conditions. Furthermore, it is also relatively easy to determine age-, size- and sex-specific reproductive success in field situations using a combination of capture–mark–recapture, field observations and molecular determinants of paternity (Zamudio and Sinervo 2000, LeBas 2002, Fitze et al. 2005, Olsson et al. 2005c, Richard et al. 2005). Coupled with the potential for experimental manipulations, this suggests that squamates could be valuable models for experimental field work on sex allocation and for disentangling the strength of multiple selection pressures, which is of outmost importance for further development of this field (Cockburn et al. 2002, Komdeur and Pen 2002).

For example, a recent study of the sand lizard, *Lacerta agilis*, addressed the issue of differential sex allocation in relation to male ornamentation using a combination of the above procedures (Olsson et al. 2005b). Experimental manipulation of male ornament size was followed by monitoring of mating behaviours under natural conditions. Females were subsequently brought in to the laboratory before oviposition where female investment is readily assessed. There was evidence for an increased investment into daughters when mated to males with large ornaments, which may be explained by a stronger negative effect of genetic quality or compatibility in daughters compared to sons (Olsson et al. 2004, 2005b). In other species, the use of semi-natural field enclosures has been successfully applied to estimate sex-specific fitness returns in relation to hatching date or to study the effect of population-specific factors such as the operational sex ratio (Le Galliard et al. 2005, Warner and Shine 2005, 2007).

While other taxa may share some of the features identified above, few offer the combination that will allow researchers to rigorously address issues in sex allocation biology.

Summary

The purpose of the present forum was threefold. (1) To argue that the present confusion in vertebrate sex allocation results from the use of very complex model systems to test relatively simple models. (2) To show that squamate model systems have been unduly neglected but show promise to tackle significant components of sex allocation theory because of their evolutionary lability of sex determination and intermediate level of complexity in life history. (3) Finally, to stimulate discussion and cross-taxonomic collaboration. We hope to show researchers working on squamate systems that their species may be well suited for sex allocation research and that this taxon is a suitable model candidate for sex allocation specialists. This may truly allow sex allocation to serve as a model phenomenon with the potential to provide us with an exceptional opportunity to understand the evolutionary process (West and Herre 2002).

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