

15 The Evolution of polyandry and patterns of multiple paternity in lizards

Erik Wapstra¹ and Mats Olsson^{2,3}

¹School of Biological Sciences, Private Bag 55, University of Tasmania, Hobart, 7001, Australia

²School of Biological Sciences, University of Sydney, Australia

³Department of Biology and Environmental Sciences, University of Gothenburg, Sweden

15.1 INTRODUCTION

The huge advances made during the 1990s in the use of molecular techniques to assign paternity within clutches/litters has led to a corresponding acceptance of the complexity of mating systems and patterns of **paternity** both within and between taxonomic groups. Perhaps most importantly this has led to a recognition of a disconnect between observed social systems (e.g., monogamous **pair bonds**) and mating systems (e.g., high rates of extra-pair paternity). It has also become clear that mating by females with multiple males leading to **multiple paternity** is taxonomically widespread (Birkhead and Møller 1998 and references therein; Jennions and Petrie 2000; Griffiths *et al.* 2002; Simmons 2005; Slatyer *et al.* 2012; Pizzari and Wedell 2013) including in lizards (Olsson and Madsen 1998; Uller and Olsson 2008). In Fig. 15.1, we have conceptualized the complex dynamics that lead to multiple paternity. At its simplest level, multiple paternity can only result if females have a mating system in which they mate with multiple different males (i.e., **polyandry**). However, the level to which multiple paternity is reflective of multiple mating will depend on post-copulatory processes including **sperm competition** and **cryptic female choice** (see Birkhead and Pizzari (2002) for review). The idea of post-copulatory female choice (i.e., cryptic female choice) is a natural extension of the vast literature on pre-copulatory female choice that occurs for both a variety of phenotypic and genetic characters (Birkhead and Pizzari 2002; see Cox and Kahl, Chapter 4 this volume). **Single paternity** arises if females choose, or are constrained, to mate with a single male within a reproductive cycle (i.e., monandry) and is also the only outcome for species with a clutch or

litter size of one. Paternity can also be skewed towards single [paternity](#) when females are polyandrous and post-copulatory mechanisms of sperm competition and cryptic female choice bias fertilization success to a single male (see Fig. 15.1).

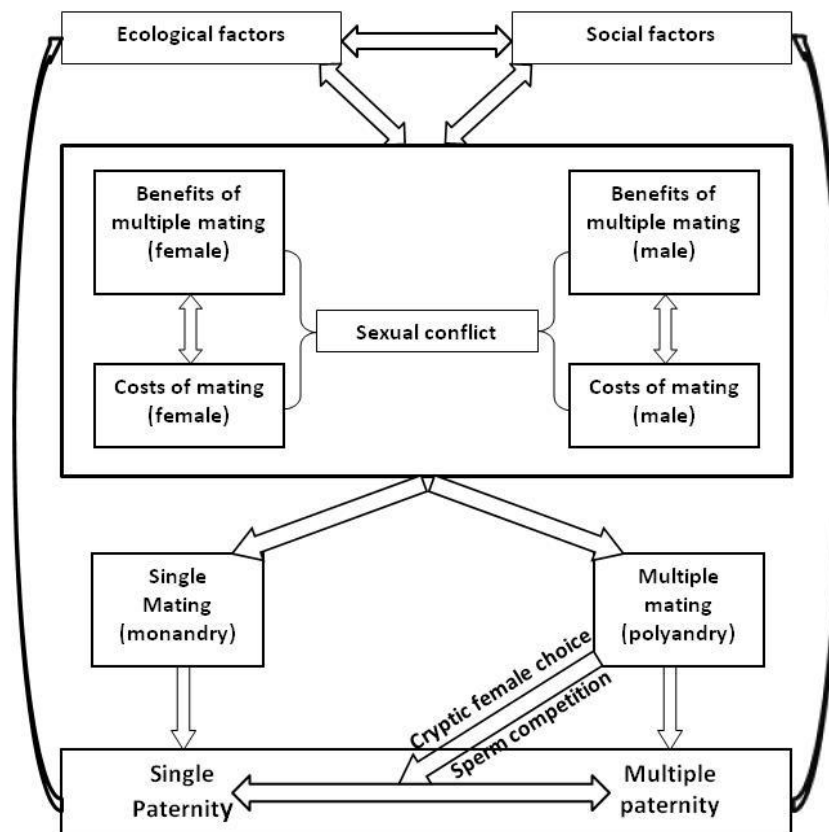


Fig. 15.1 Conceptual diagram depicting the complex evolutionary and ecological landscape leading to multiple paternity. Multiple paternity is a consequence of ecological and social factors that dictate the relative costs and benefits of multiple mating males and females. The resolution of the sexual conflict between optimal mating rates largely dictates if mating will be monandrous or polyandrous. If mating is polyandrous, the post-copulatory phenomena of sperm competition and cryptic female choice will dictate the degree of that polyandry is reflected in multiple paternity.

Polyandrous mating was traditionally explained through classic [sexual selection theory](#) (e.g., Bateman's Principle; Bateman (1948)) based on the premise that a male's reproductive rate is limited by access to females willing to mate, whereas a female's reproductive success is limited to access to material resources she can convert into offspring rather than access to males/sperm (Bateman 1948; Trivers

1972; Andersson 1994; Simmons 2005; Parker and Birkhead 2013; Pizzari and Wedell 2013; see also Cox and Karhl, Chapter 4 this volume). Under this view, polyandrous mating is a consequence of [sexual conflict](#) where males seek to mate multiple times to maximize their reproductive output with females passively accepting male mating with little to no benefit in order to reduce the potential cost of the conflict (Fig. 15.1; Andersson 1994). However, with the growing empirical evidence that female multiple mating is widespread this view has changed and there is growing appreciation that females do benefit from mating with several males within a reproductive cycle (i.e., polyandry). While multiple paternity across all taxonomic groups studied to date point to widespread polyandry, understanding the evolutionary and ecological conditions under which polyandry benefit the females remains a major challenge of evolutionary biology (Simmons 2005; Eizaguirre *et al.* 2007; Uller and Olsson 2008; Alonzo 2010; Slatyer *et al.* 2012; Pizzari and Wedell 2013).

The majority of work aimed at addressing the questions of why females mate with multiple males has revolved around three main hypotheses. These non mutually exclusive hypotheses suggest that polyandry evolves because it: 1) directly increases female fitness through increases in [fecundity](#) or survival; 2) indirectly increases female fitness through genetic benefits to offspring; or 3) evolves through sexual conflict over optimal mating rates where females mate multiply to minimize negative costs associated with avoiding multiple matings (convenience polyandry) (see below). To sort between the relative importance of these hypotheses, we need to appreciate that mating is the outcome of a two players game, a male and a female, and thus will ultimately be dictated by the costs and benefits to each player (Arnqvist and Kirkpatrick 2005).

When the cost and benefits differ between the sexes, sexual conflict arises (Fig. 15.1). The resolution of these costs will invariably be context-dependent and result in variation in levels of multiple paternity. Thus, understanding patterns of paternity will benefit from a perspective that takes into account direct and indirect fitness costs and benefits of mating strategies and the way they feed back with ecological and social factors (Badyaev and Qvarnstrom 2002;

Cornwallis and Uller 2010; Oh 2011; Holman and Kokko 2013; Fig. 15.1). Furthermore, we need to recognize that evolutionary and ecological drivers of male and female multiple mating (polygyny and polyandry) operate at multiple scales from the individual female (shaping variation in polyandry among females), populations (shaping variation in polyandry among years within populations and between populations) and species (shaping variation in polyandry between species)(see Botero and Rubenstein 2012; Bonier *et al.* 2014).

Ultimately, providing a unified framework for understanding patterns of multiple paternity across taxa is of fundamental importance to evolutionary biologists. This is because female polyandry, and female mating behavior more generally, can have significant implications for the evolutionary trajectory of populations (Price *et al.* 2010, Cornwallis *et al.* 2010; Holman and Kokko 2013). For example, explaining the variation in patterns of multiple paternity is being increasingly recognized as important because of its role in driving within family/group relatedness and the consequence this has for understanding the emergence and diversification of social systems and behavior, including investment in parental care and cooperation (Hughes *et al.* 2008; Cornwallis *et al.* 2010; Griffin *et al.* 2013; Lukas and Clutton-Brock 2013; Pizzari and Wedell 2013).

15.2 PATTERNS OF PATERNITY IN LIZARDS

While documentation of patterns of paternity in lizards (and reptiles more generally) falls well behind many other taxa, such as birds and invertebrates, in terms of numbers of studies or diversity of species (compare for example Griffiths *et al.* 2002 with Uller and Olsson 2008), multiple paternity has been shown in all lizards studied to date (see Table 15.1 and Uller and Olsson 2008) and this reflects similar data for other reptilian taxa (e.g., natricine snakes; Wusterbarth *et al.* (2010)). What is also clear is that levels of multiple paternity in lizards are generally high but vary among individuals within populations, among populations within species, and among species (Table 15.1 and references therein and Uller and Olsson 2008). These patterns reflect the outcome of multiple ecological and social selective pressures as well as the outcome of sexual conflict between optimal

mating rates (Fig. 15.1). In field correlative studies, demonstration of multiple paternity is an outcome of females mating with different males but otherwise the processes remain largely a “black box” representing a range of processes with mate encounter rate, [mate choice](#), sperm competition, cryptic female choice, and potential embryo loss all potentially contributing to the observed patterns. To address this, research has moved towards more experimental approaches where competing hypotheses on costs and benefits of polyandry (especially from the female perspective), along with proximate and physiological mechanisms behind it, can begin to be teased apart (e.g., Fitze *et al.* 2005; LaDage *et al.* 2008; Le Galliard *et al.* 2008; Keogh *et al.* 2013; Noble *et al.* 2013).

Table 15.1 Patterns of multiple paternity in lizards from natural populations. Only studies where all offspring were known are included (typically because all eggs from a clutch were collected or females gave birth in the laboratory). In some cases multiple paternity is reported but paternity of individual offspring is unknown. Table based on Uller and Olsson (2008), and extensive literature searches conducted to update the information to 2013. Experimental manipulations (even in large field enclosures) where patterns of paternity are expected to deviate from natural conditions (adult sex ratios, unnatural densities, restricted mate choice, costs of mating) have not been included.

Taxon	% multiple paternity	# clutch examined	Reference
Scincidae			
White's skink, <i>Egernia whitii</i>	12	50	Chapple and Keogh 2005
White's skink, <i>Egernia whitii</i>	17	90	While et al. 2009a
Spiny-tailed skink, <i>Egernia stokesii</i>	25	16	Gardner et al. 2000; 2002
Cunningham's skink, <i>Egernia cunninghami</i>	3	38	Stow and Sunnucks 2004
Sleepy lizard, <i>Tiliqua rugosa</i>	19	21	Bull et al. 1998
Southern water skink, <i>Eulamprus heatwolei</i>	65	17	Morrison et al. 2002
Blue Mountains water skinks, <i>Eulamprus leuraensis</i>	27	11	Dubey et al. 2011
Southern snow skink, <i>Niveoscincus microlepidotus</i>	75	8	Olsson et al. 2005c
Grand skink, <i>Oligosoma grande</i>	47	15	Berry 2006
Mt log skink, <i>Pseudomoia eurecateuixii</i>	53	17	Stapley et al. 2003
Spanish rock lizard, <i>Iberolacerta cyreni</i>	48	33	Salvador et al. 2008
Common five lined skinks, <i>Plestiodon fasciatus</i>	65	20	Bateson et al. 2011
Lacertidae			
Common lizard, <i>Lacerta vivipara</i> ¹	67	46	Eizaguirre et al. 2007
Common lizard, <i>Lacerta vivipara</i> ²	47	51	Eizaguirre et al. 2007
Common lizard, <i>Lacerta vivipara</i> ³	55	38	Eizaguirre et al. 2007
Common lizard, <i>Lacerta vivipara</i>	65	26	Hofmann & Henle 2006
Common lizard, <i>Lacerta vivipara</i> ^{p1}	68	458	Laloi et al. 2004
Common lizard, <i>Lacerta vivipara</i> ^{p2}	50	15	Laloi et al. 2004
Common lizard, <i>Lacerta vivipara</i>	54	54	Richard et al. 2012
Common lizard, <i>Lacerta vivipara</i>	unreported	unreported	Laloi et al. 2009
Sand lizard, <i>Lacerta agilis</i>	80	5	Gullberg et al. 1997
Sand lizard, <i>Lacerta agilis</i>	unreported	unreported	Olsson et al. 2011a, b
Common wall lizard, <i>Podarcis muralis</i>	87	31	Oppliger et al. 2007
Agamidae			
Ornate dragon, <i>Ctenophorus ornatus</i>	25	20	Lebas 2001
Painted dragon, <i>Ctenophorus pictus</i>	18	51	Olsson et al. 2007
Phrynosomatidae			
Striped plateau lizard, <i>Sceloporus virgatus</i>	61	13	Abell 1997
Side-blotched lizard, <i>Uta stansburiana</i>	72	123	Zamudio & Sinervo 2000
Iguanidae			
Black spiny tailed iguana, <i>Ctenosaura pectinata</i>	11	10	Faria et al. 2010

¹ Refers to first year of study ² Refers to second year of study ³ Refers to third year of study ^{p1} Refers to population 1 ^{p2} Refers to population 2

Why is multiple paternity common in lizards (and reptiles more generally)? Are there particular features of their biology that make them likely to undertake multiple mating leading to multiple paternity? With the exception of a restricted number of lizard taxa that show complex forms of long term social bonds (see While *et al.*, Chapter 16 this volume), which in other taxa (including mammals and birds) reduces selection and opportunity for multiple mating, the majority of lizard mating systems can be typified by intense [male-male competition](#) for females via direct [male-male conflict](#) or resource-driven [polygyny](#) (see Olsson and Madsen 1998 and Cox and Kahrl, Chapter 4 this volume). Another feature of lizard mating systems is the near ubiquitous presence of [sperm storage](#) by females (see Olsson and Madsen 1998; Sever and Hamlett 2002). Sperm storage provides an extended temporal window for multiple mating that leads to opportunities for multiple mating (by dissociating to some extent the temporal window of receptivity with fertilization). Sperm storage following polyandrous mating leads to enhanced opportunities for [sperm competition](#) and cryptic female choice, both of which are central to hypotheses for the evolution of [polyandry](#) (see below).

As storage of sperm of multiple males by females is common, there should be concomitant selection on males to minimize their paternity loss to other males (see Olsson and Madsen 1998; Simmons 2005). These processes can occur pre- or post-copulatory and include male mate choice, sophisticated sperm expenditure including altered ejaculate size, [copulatory plugs](#), male [mate guarding](#), increased testis size, and selection on sperm morphology (Olsson and Madsen 1998). What is clear is that despite ongoing selection on males to maximize their share of paternity through such mechanisms as mate guarding (including social monogamy), high levels of multiple paternity within clutches/litters is still the common pattern (Bull *et al.* 1998; Olsson *et al.* 2005a; While *et al.* 2009a, b; Ancona *et al.* 2010).

Table 15.1 shows the limited number of studies (up to and including 2013) that report multiple paternity under field conditions. Further experimental work examining the fitness benefits of polyandry are discussed in further sections addressing support for alternate

hypotheses for the evolution of polyandry. Despite the growing number of studies detailing patterns of paternity in lizards in both field and experimental studies, there are still considerable gaps in the literature for the majority of species. Indeed, current research into multiple paternity in lizards exhibits a strong taxonomic bias (Table 15.1). This presents significant challenges when trying to make broad phylogenetic inferences on variation in patterns of paternity across lizard lineages. For example, more than 75% of the studies are restricted to three families of lizards (skinks, lacertids and [agamids](#)) and for the vast majority of families we have next to no data on patterns of paternity, or the ecological or evolutionary factors that may promote it. Furthermore, nearly a quarter of the studies to date have centered on the *Egernia*-group of skinks in Australia (Table 15.1; Uller and Olsson 2008). The *Egernia*-group have been utilized heavily as model organisms for studies related to the evolution of sociality, mating systems and parental care; traits which are expected to co-vary with benefits to multiple mating (e.g., Bull *et al.* 1998; Chapple 2003; Chapple and Keogh 2005; While *et al.* 2009a, b; 2011; 2014; *see* While *et al.*, Chapter 16 this volume). For example, patterns of paternity and parental care are predicted to co-evolve because the former dictates the cost–benefit ratio of the latter by affecting genetic relatedness between adults and offspring (Griffin *et al.* 2013). It is unfortunately premature to undertake a sufficiently rigorous meta-analysis on the limited number of empirical studies (or experimental studies) that document patterns of paternity in lizards to separate out competing hypotheses for the evolution of polyandry and paternity in lizards. What is clear is that lizard social and mating systems and reproductive cycles are diverse (more so than has been traditionally accepted; Doody *et al.* 2013) and thus we would expect a variety of patterns of paternity to emerge with potentially a variety of selective forces shaping those patterns.

As outlined in other chapters in this book, lizards have already made an impact on our understanding of key processes including sexual selection, mating systems, reproductive allocation, sex allocation and parental care. Below we show that lizards have also provided good model systems to further our understanding of the

benefits of polyandry and multiple paternity. Given the limited taxonomic coverage and only recent move to experimental approaches, valuable models for understanding the evolution of polyandry and multiple paternity are still left ready for exploitation. Below we briefly review alternate hypotheses for multiple paternity and indicate where lizards have either contributed to our understanding or have the potential to do so.

15.3 ASSESSING EVIDENCE FOR THE HYPOTHESES FOR MULTIPLE PATERNITY IN LIZARDS

Patterns of polyandry reflect the resolution of the sexual conflict between male mating rates (driven by costs and benefits to males) and female mating rates (driven by cost and benefits to females). In principle, the reasons males mate multiply is non-contentious – the more females they mate with the higher their reproductive output. While this may be balanced to some extent by high costs of mating and may result in careful mate choice and sophisticated sperm expenditure, in general males benefit strongly from multiple mating. Sexual selection in reptiles has been examined previously (Olsson and Madsen 1998) and has been recently re-examined in detail for lizards by Cox and Kahrl (Chapter 4 this volume). Given their concentration on sexual selection from the male perspective including both pre- and post-copulatory phenomena, where appropriate in this chapter we refer readers to their chapter. To prevent overlap between chapters, we concentrate on hypotheses explaining polyandry and multiple paternity from the female perspective.

Given the potential costs associated with multiple mating (e.g., energetic cost, loss of feeding opportunity, disease transmission, injury and increased risk of predation (Olsson and Madsen 1998; Watson *et al.* 1998; Eizaguirre *et al.* 2007; Madsen 2011; Slatyer *et al.* 2012), and that females immediate reproductive output is not enhanced as directly as males by multiple mating, explanations for female multiple mating are typically divided into three main adaptive hypotheses (Jennions and Petrie 2000; Eberhard and Cordero 2003; Simmons 2005; Uller and Olsson 2008; Slatyer *et al.* 2012). We address these hypotheses below firstly by describing the underlying theory and empirical support from other taxa and then we submit the

hypotheses to scrutiny using field and experimental studies from lizards.

15.3.1 Polyandry through direct benefits

Females may benefit directly from multiple mating because they receive direct material benefits from males (Fedorka and Mousseau 2002). These can include [nuptial gifts](#), nutrients in ejaculates, or increased male provisioning to either the female or her offspring (see Andersson 1994; Birkhead and Møller 1998; Gwynne 2008). In this scenario, multiple mating results in increased transfer or access to male resources that increase either a female's fecundity or survival (increasing reproductive potential into future years). Such direct benefits are especially common in birds and insects (see Vahed 1998; Arnqvist and Nilsson 2000). A key to understanding the situations where this scenario leads to polyandry (i.e., multiple mating with different males rather than the same male) is to separate out the effects of multiple mating *per se* with the benefits of mating with multiple males (LaDage *et al.* 2008). The potential for direct fitness gains to females from mating with different males must be balanced against potential fitness costs. In birds, for example, mating with different males could benefit the female if it leads to enhanced offspring care because there are more males to provide the care but there may be costs associated with the cuckolded male potentially reducing provisioning (Kokko 1999; Griffin *et al.* 2013 and references therein).

In lizards, we can largely rule out hypotheses centered on females receiving direct material benefits from nuptial gifts, ejaculate nutrients and extended paternal assistance; males do not provide nuptial gifts and there is no evidence in lizards that energy contained in ejaculates is either available to females, or sufficient in terms of energy, to increase their reproductive efforts (Olsson *et al.* 2004b; Uller and Olsson 2008; Eizaguirre *et al.* 2007). Furthermore, in reptiles male [parental care](#) of offspring is rare (but see While *et al.*, chapter 16 this volume) and where rudimentary care of offspring through protection from conspecifics or predators does occur (mostly in *Egernia* skinks; O'Connor and Shine 2004; Sinn *et al.* 2008), it appears to select against multiple mating by females (While *et al.* 2009b). Therefore,

direct benefits as a potential factor influencing the evolution of polyandry is unlikely in lizards.

An extension of the hypothesis that polyandry is driven by direct benefits to females is that multiple mating may confer a direct fitness gain if it maximizes the provision of fertile sperm or reduces the risk infertile sperm (e.g., assurance of [fertilization](#), Sheldon 1994; Wedell *et al.* 2002; García-González and Simmons 2005). While levels of [infertility](#) in lizards has not been examined extensively, in sand lizards (*Lacerta agilis*), levels of infertility in males (which would select for female multiple mating) is very low in the natural population and is unlikely to play a role in the evolution of polyandry (Olsson and Shine 1997). However, males may be infertile (immature sperm) early in the season when they emerge from hibernation and this may drive temporal patterns of mating as well as patterns of sex-specific emergence in sand lizards (Olsson and Madsen 1996) and Southern snow skinks (*Niveoscincus microlepidotus*) (Olsson *et al.* 1999). In other taxa, there is evidence that females can benefit from multiple mating through increased fecundity or fertility; in common lizards (*Lacerta vivipara*), Eastern water skinks ([Eulamprus quoyii](#)) and in leopard geckos ([Eublepharis macularius](#)) multiple mating leads to higher reproductive output and this has been implicated in these species in the evolution of polyandry (Uller and Olsson 2005; LaDage *et al.* 2008; Noble *et al.* 2013). However, as an explanation for the widespread occurrence of polyandry in lizards it remains unsupported because of poor taxonomic coverage exploring this phenomenon in general (Sheldon 1994; Slatyer *et al.* 2012) and in lizards (Noble *et al.* 2013). In lizards, the scenarios in which females would be most susceptible to inadequate sperm transfer are predicted to include those with short mating seasons, those where encounter rates are low or unpredictable, when copulations result in inadequate sperm transfer, and/or males vary in sperm quality (Noble *et al.* 2013): these data are either not available for many lizards or have not been used to test this hypothesis more broadly.

15.3.2 Polyandry through indirect genetic benefits

The second set of hypotheses for the evolution of polyandry center on the indirect genetic benefits derived from elevated mean offspring fitness (and therefore parental [fitness](#)) potentially because the presence of sperm of multiple males opens up the opportunity for sperm competition and [cryptic female choice](#) (Jennions and Petrie 2000; Zeh and Zeh 2003; Slatyer *et al.* 2012). This can lead to increased female fitness via increased [genetic diversity](#) of offspring (genetic bet-hedging), increased offspring quality through fertilization by higher quality males (e.g., sexy sperm hypothesis or “trade-up” hypothesis), avoidance of genetic incompatibility through egg/sperm incompatibility and/or cryptic female choice, or increased level of genetic compatibility/complementarity, or [inbreeding avoidance](#) (Zeh and Zeh 1996; Jennions and Petrie 2000; Neff and Pitcher 2005; 2008; Uller and Olsson 2008; Puurtinen *et al.* 2009; Slatyer *et al.* 2012; Noble *et al.* 2013). Many of these hypotheses are logical extensions of the hypotheses for female pre-copulatory mate choice (over one partner) and may be especially important where initial female choice is constrained by social or ecological factors. Importantly, these hypotheses on indirect genetic benefits predict that offspring from polyandrous females should have increased fitness, on average, compared with singly mated females. Some of these effects could arise simply through sperm competition; however, multiple mating provides the opportunity for females to use cryptic mate choice to bias paternity towards males that elevate offspring fitness.

Indirect genetic benefits for polyandry remains controversial (e.g., Yasui 1998) with both empirical studies and recent meta-analyses providing mixed support (e.g., Simmons 2005; Fisher *et al.* 2006; Hettyey *et al.* 2010; Slatyer *et al.* 2012). For example, recent meta-analyses on birds provided weak support for indirect benefits as an explanation for multiple mating (Arnqvist and Kirkpatrick 2005; Akçay and Roughgarden 2007), while a meta-analyses on insects suggested that polyandry was associated with increased hatching success (Simmons 2005). The equivocal support might be because of taxonomic differences in life history and reproductive strategies. For example, in birds and mammals, sophisticated (bi)[parental care](#) may make it comparatively more difficult to pick-up subtle differences in

offspring fitness arising through indirect genetic effects than in insects where maternal provisioning usually ends at hatching or birth (but see Simmons 2005). Therefore, tests of polyandry-derived genetic effects on offspring fitness may be compromised (except in artificially controlled situations) by patterns of parental investment (i.e., maternal and paternal effects) where higher levels of investment, for example, may increase offspring fitness masking or exaggerating the genetic effects. Parental investment can vary according to genetic or phenotypic quality of partner, relatedness, and levels of paternity assuredness in the litter/clutch (e.g., Senar *et al.* 2002; Horvathova *et al.* 2012).

In some taxa, these adjustments can occur at multiple stages. In birds, for example, altered allocation patterns can be achieved by adjusting investment (i.e., egg size) within and between clutches and/or adjusting post-hatching feeding rate and food quality within and between clutches. Similarly in mammals, investment can be altered at several developmental stages including pre-birth, during gestation and certainly via maternal provisioning post birth (Hewison and Gaillard 1999). Clearly, the multitude of levels of investment may allow parental adaptive control over offspring fitness, but it also severely compromises the potential to make *a priori* predictions regarding the direction and magnitude of indirect genetic effects at a given level of investment. Female allocation patterns are more straightforward in lizards (but see Uller and While, Chapter 13 this volume) and complications arising from male parental effort largely non-existent (see below). We suggest that lizards could be valuable models for disentangling the importance of indirect genetic effects of male and female multiple mating which is of utmost importance for further development of this field.

Broadly, there is support for the importance of indirect genetic effects in lizards (and more broadly in reptiles). Reptiles (particularly adders, *Vipera berus*, sand lizards, *Lacerta agilis* and side-blotched lizards, *Uta stansburiana*) certainly played a key role in formulating our thinking that multiple mating can have a positive effect on female fitness (Madsen *et al.* 1992; 1999; 2004; Olsson *et al.* 1994a; 1994b; 1996; 2005b; Zamudio and Sinervo 2000; Olsson and Madsen 2001;

Calsbeek and Sinervo 2002; 2004; Sinervo *et al.* 2006) through enhanced offspring viability or survival. However, it has since been debated whether these indirect genetic effects were detected (or even occurred) more readily because the populations used in these studies have low genetic diversity (see Madsen 2008; Olsson and Uller 2009) or potentially in the case of side-blotched lizards because polymorphisms create strong sire effects. Does this mean that indirect genetic benefits as a result of polyandrous mating are rare in lizards? Recent work would suggest not, with evidence from other lizard species indicating that multiple mating by females increases offspring fitness.

Recent studies of the European common lizard (*Lacerta vivipara*) established that while polyandry and monandry coexist among females (Laloi *et al.* 2004), polyandry confers fitness benefits (Fitze *et al.* 2005). Specifically, Eizaguirre *et al.* (2007) demonstrated that polyandrous females produce larger [clutches](#) than monandrous females (controlling for number of matings) and that embryo mortality during late stages of development was also reduced in polyandrous clutches. With their field-based study, they were not able to separate out the competing hypothesis of genetic compatibility, intrinsic male quality or inbreeding avoidance as the causal mechanism. In field studies, other potential fitness effects of multiple mating have been demonstrated with dispersal being greater in polyandrous litters than in [monandrous litters](#) (Laloi *et al.* 2009), which may affect a range of demographic processes including female-offspring competition (see Chapple and Keogh 2005 for links between polyandry versus monandry and sex biased dispersal in the White's skink, *Egernia whitii*). Recent work on the common lizard has also provided evidence consistent with the hypotheses that [multiple mating](#) provides an opportunity for females to genetically "trade-up" (Laloi *et al.* 2011; see also Fitze *et al.* 2010). They found that females preferentially accepted males of higher [heterozygosity](#) (presumably resulting in higher quality offspring) for second matings. Similarly, While *et al.* (2014) showed that female multiple mating in White's skink may serve as an inbreeding avoidance mechanism. Specifically, there were high levels of relatedness between male and female pairs as a result of

strong genetic structure within the population. Females alleviate the constraints of social mate choice imposed by population viscosity by mating outside their pair bond with less related males. As a result offspring from extra-pair males exhibited a significantly increased genetic diversity compared to within-pair offspring.

Recent models predict such female choosiness and “trade-up” decisions (Bleu *et al.* 2012) but also that choosiness should be context-dependent: females gain greater benefits from such choosiness when encounter rates or the cost of mating is high. Context-dependent mate choice (especially context-dependence of choice of second or third mates) remains largely untested in lizards. Until the mid 90s, widespread evidence for pre-copulatory mate choice was considered weak in reptiles (Olsson and Madsen 1995; Tokarz 1995), however since then increasing evidence for choice using olfactory cues, including potentially at the Major Histocompatibility Complex (MHC), has been demonstrated (e.g., Lopez *et al.* 2003; Olsson *et al.* 2003) suggesting that mechanisms for sophisticated female (and male) decisions exist. For example, Martin and Lopez (2013) demonstrated (in an experimental context) that female Carpetan rock lizards (*Iberolacerta cyreni*) preferred scents of large territorial males over smaller males but they also preferred areas with scents of multiple males. They suggested this latter result may increase the probability of obtaining multiple copulations with different males, which may favor sperm competition and cryptic female choice. For a more extensive discussion of the role of pheromones in lizard communication, including its important role in mate choice and intersexual competition (see Martin and Lopez, Chapter 3 this volume).

Cryptic female choice is the logical extension of female pre-copulatory choice and has been argued as one of the most likely benefits of female multiple matings in lizards (see Olsson *et al.* 1994a; 1996; Olsson and Madsen 2001), especially when evidence of female pre-copulatory choice in lizards was lacking. While there is compelling evidence for cryptic female choice, including sophisticated matching of sperm from different males to offspring sex (Calsbeek and Sinervo 2004; Corl *et al.* 2012; Calsbeek and Bonneaud 2008; Olsson *et al.* 1994a; b; 1996; 2004b; 2005a), it is difficult to reconcile

the ubiquitous nature of multiple paternity in lizards (at very high levels) with this idea (Uller and Olsson 2008). If, in general, cryptic female choice was strong (and effective), paternity skews should be high (biased towards the female's favored genetic partner) yet this is not the generally observed pattern with levels of multiple paternity generally high (Uller and Olsson 2008; Table 15.1). Furthermore, without information on what the paternity skew is expected to be from the female's fitness perspective (e.g., based on theoretical or empirical predictions of fitness effects for different sires), it is difficult to easily demonstrate cryptic female choice in lizards because paternity skews can arise from a host of other factors that affect the outcomes of sperm competition.

In order to separate out evidence for cryptic female choice from outcomes of sperm competition, there are some logistical constraints to overcome that are challenging for lizards. Firstly, we need information on how many times a female has copulated; secondly we need information on which males she has copulated; thirdly we need to have information on how many sperm each male transferred during copulation; and, finally we need information on variation in sperm morphology and behavior between males (see for example extensive review by Snook 2005). The first is often easy in lizards as [copulation](#) can leave distinct copulation marks from the male biting the female (e.g., Fitze *et al.* 2005; While and Wapstra 2009). The second challenge to assess which males a female has mated with presents greater challenges because this information must not be inferred from molecular techniques but must be directly obtained from observations of copulations. In the majority of lizards, this information is difficult in the field or semi-natural enclosures because copulations are generally cryptic and occur relatively quickly (Olsson and Madsen 1998; While and Wapstra 2009). In the laboratory, these processes can be more readily observed and has the added advantage that male-female [relatedness](#), female pre-copulatory choice and mating order can be controlled (but with a loss to realism). Knowing the amount of [sperm](#) transferred by males during copulation presents the greatest logistical challenges in lizards because of internal fertilization (compare the ease with which paternity skews can be assessed with

external fertilizers such as frogs for example; Sherman *et al.* 2008; 2009). In reptiles, there is limited data to suggest that copulation duration is related to sperm transfer (Olsson and Madsen 1998; Olsson 2001; Shine *et al.* 2000; Olsson *et al.* 2004a), but this does not take into account inter-male differences in sperm count nor the sophisticated nature of sperm allocation (even between ejaculates) that can occur (e.g., Olsson 2001; Olsson *et al.* 2004a; Uller *et al.* 2013; see Snook 2005 for an extensive review).

15.3.3 Evolution of polyandry through sexual conflict

This hypothesis suggests that because there is sexual conflict over mating rates, a female is faced with a trade-off between resisting male mating and incurring the costs associated with harassment and even forced copulations or minimizing these costs by accepting the mating (“convenience polyandry”; Slatyer *et al.* 2012). In this situation, polyandry can arise without any fitness gain to the female in terms of direct or indirect fitness gains, however, fitness “loss” is minimized. This explanation requires that the costs to males mating multiply are significantly lower than those of females and that the reduction in fitness from multiple mating to females (through, for example, increased disease risk, injury, predation, and energy use) are less than the costs associated with avoidance of multiple mating. Understanding the adaptive scenario where this may arise relies on detailed knowledge of the costs of multiple mating to the female (e.g., energy, predation risk, disease transmission, poor genetic compatibility) against the costs of male harassment and/or potential forced copulation (see Arnqvist and Rowe 2005 and references therein). Embedded into the logic of this hypothesis is that any factor that alters the optimal mating rate for males (including for example density effects or contact rates), will, in the absence of altered costs or benefits to females, affect the mating rate between males and females (i.e., the degree of polyandry).

In a review of multiple mating in reptiles, Uller and Olsson (2008) suggested that despite the emerging evidence for indirect genetic effects in reptiles, compelling evidence for indirect genetic effects driving polyandry in reptiles was weak. They suggested that the most

parsimonious explanation for the frequent and high levels of polyandry was that it represented a combined effect of mate-encounter frequency and conflict over mating rates between males and females driven by large male benefits and relatively small costs to female mating. In part, their view is based on the evolutionary origin of polyandry via male-driven selection and the idea that female benefits arise later (see Olsson and Uller 2009 for a more detailed argument). The key to understanding the role of convenience polyandry is an acceptance that additional mating invariably will carry a cost but that cost, in relation to the costs of harassment and the potential gains in indirect fitness, is low (see also Fitze *et al.* 2005; Uller and Olsson 2009; Le Galliard *et al.* 2008; Madsen 2011). Potential costs to females with increased contact with males could include disease transmission. In sleepy lizards (*Tiliqua rugosa*) and in Tuatara (*Sphenodon punctatus*), there is evidence that contact between individuals, including potentially during mating, is related to parasitic and bacterial infection (Godfrey *et al.* 2009; 2010; Leu *et al.* 2010; Fenner *et al.* 2011; Bull *et al.* 2012). In addition, multiple mating may confer increased risks of predation to females, as has been demonstrated in adders (*Vipera berus*; Madsen 2011), but data in lizards are currently lacking.

Experimental approaches on common lizards (*Lacerta vivipara*) using large semi-natural enclosures have been instrumental in advancing our understanding of the role of sexual conflict and the costs of mating and female benefits. By manipulating adult sex ratios, a series of studies showed that while overall polyandry was associated with larger clutches (as also detailed above), male biased populations led to higher rates of copulation through sexual harassment and that females from these populations had lowered reproductive success and survival (Fitze *et al.* 2005; Le Galliard *et al.* 2005). In follow-up work, Le Galliard *et al.* (2008) examined if the direct costs of increased male harassment on female reproductive success and survival were mitigated by indirect benefits through offspring growth, offspring survival or mating success; they were not, leading them to conclude that their observations of conflict over mating rates arise because fitness gains are greater in males than the net costs to females.

Our own work in natural populations of sand lizards (*Lacerta agilis*) also emphasizes the importance of proximate factors in determining male and female encounter rates and concomitant rates of multiple paternity. In a decade-long study in their natural environment in Sweden we showed that increased temperature during the spring mating season increased mating rates and the numbers of sires per clutch. In our case, this had positive effects on indirect measures of fitness including a reduction in malformations within clutches and increased offspring survival (Olsson *et al.* 2011a, b). Thus, in warm years when activity and encounters between males and females are high, there was evidence of positive indirect fitness benefits to females and in contrast to the work in outdoor enclosures, direct costs to females were not evident probably because harassment costs could be avoided by avoidance and fleeing. Recently, Keogh *et al.* (2013) also emphasized the importance of male encounter rates with females as a predictor of reproductive success in the Australian Southern water skink (*Eulamprus heatwolei*) concluding that female multiple mating was best explained by the combined effect of mate encounter frequency and high benefits to males but low costs to females.

15.4 TOWARDS A HOLISTIC UNDERSTANDING OF PATTERNS OF PATERNITY IN LIZARDS

Polyandry leading to [multiple paternity](#) is widespread in lizards but its explanation remains controversial (Uller and Olsson 2008; Madsen 2008; Olsson and Uller 2009; Madsen 2011; Noble *et al.* 2013). This controversy is driven, in part, by the ongoing debate more broadly on what selective forces lead to polyandry and why patterns may differ among females, populations, species, and episodes of selection (e.g., years/mating seasons) (e.g., Simmons 2005; Slatyer *et al.* 2012; Parker and Birkhead 2013). We would argue that the central question of whether females mate multiply to gain direct fitness gains, indirect genetic fitness gains or to reduce the costs of male harassment is unsatisfactory – in many taxa all of these explanations are relevant and involved in explaining observed patterns. As Parker and Birkhead (2013) elegantly argue the “why polyandry” for a given population (or species) can only be addressed by analysis of the distribution of all possible state-dependent encounters between pairs of males and

females in a population (see also Alonzo and Sinervo 2001). Each of these encounters then has a probability of resulting in a mating depending on the sum of costs and benefits to the male and female involved and the resolution of the conflict over these. The sum of the probabilities of encounters and the mating outcomes will result in observed mean level of polyandry in the population (Parker and Birkhead 2013). The level to which polyandry then results in multiple paternity will then be dependent on the post-copulatory phenomena of sperm competition and [cryptic female choice](#).

This verbal argument is necessarily individual, population, and species-specific from the outset and its simplicity hides a multitude of ecological and evolutionary factors (Fig. 15.1). For example, in lizards, a host of behavioral (e.g., movement rates, social and mating systems), demographic (e.g., density, frequency of reproduction, operational sex ratios) and ecological factors (e.g., habitat complexity, weather dependent activity patterns) affect encounter rates between males and females and these feed back on each other in complex ways. Demonstrating the relative costs and benefits of mating to each sex is equally complex, taxon-specific, and will covary with mating system and level of inbreeding. There is little doubt that both males and females incur mating costs that are more than offset by the benefits of multiple mating (hence the ubiquitous patterns of multiple paternity) but we are in our infancy in understanding what affects the sum of these for either of the sexes (which determines the asymmetry in the optimal mating frequency), *let alone* the combined sum for these which resolves the sexual conflict. We agree with Pizzari and Wedell (2013) that studies considering the evolutionary ecology of polyandry (and the outcome of multiple paternity) with a wider, interdisciplinary context have much to offer in advancing our understanding. Specifically we require a tighter connect between proximate studies of costs and benefits with studies measuring fitness consequences under realistic conditions.

15.5 FUTURE DIRECTIONS

Below we provide some key future directions for studying patterns of paternity in lizards that will broaden our taxonomic understanding

and move to address the complexity of factors that influence multiple mating and multiple paternity in lizards.

15.5.1 Broader taxonomic coverage

As has been advocated by the recent surge in reviews and meta-analyses within and across taxa, a broad taxonomic coverage is required to provide insights that are hidden from a specific taxonomic perspective, particularly the contexts in which polyandry may arise through selection on males versus females. Specifically, in lizards we lack data on a large number of families and within the more well studied families (e.g., lacertids and skinks), research is biased towards a limited number of species (e.g., *Lacerta vivipara* and *Lacerta agilis* in the lacertids and the Egernia-group in skinks).

15.5.2 More long-term field studies and assessment of offspring fitness in the wild

Ultimately, addressing the adaptive hypotheses for polyandry/multiple paternity should ideally occur under natural (preferably) field conditions because field patterns will reflect the ecological and social factors that influence encounter rates, and the sum of the costs and benefits to both sexes. If multiple paternity is in part driven by offspring fitness (which we predict them to be), field studies can also provide realistic tests of fitness under realistic conditions. This has proven a major obstacle in many insects, bird, and mammal systems because it is often difficult to assess long-term fitness of offspring (e.g., Cockburn *et al.* 2002, Komdeur and Pen 2002). Many lizards are relatively conspicuous animals with restricted dispersal and territoriality (and geographically small home ranges) therefore it is relatively easy to assess offspring survival and male and female reproductive success using a combination of capture-mark-recapture, field observations, and molecular determinants of paternity (e.g., Zamudio and Sinervo 2000; Pen *et al.* 2010; Olsson *et al.* 2011a, b; Uller *et al.* 2011; While *et al.* 2014).

One of the major challenges with understanding patterns of multiple mating in lizards is the lack of long-term studies which report variation in patterns of paternity between years and between populations (but for recent examples see Eizaguirre *et al.* 2007; While

et al. 2009a; 2011; Olsson *et al.* 2011a, b). Long term field studies have the potential to reveal ongoing (and fluctuating) selection on mating patterns as well as potential external factors that may affect encounter rates. Currently, too many of the field studies (again noting the relative paucity of work on lizards in general) represent snapshots in time.

15.5.3 Greater emphasis on linking experimental approaches with field approaches:

Field studies (with a greater taxonomic coverage) will provide us with the patterns of polyandry and multiple paternity that are required to establish taxon-relevant hypotheses best tested with experimental manipulations. Because of the ease with which lizards can be monitored in the field, they have the added advantage that they are suitable for experimental field work which will be crucial as we advance from correlative field approaches. Lizards offer a suite of potentially powerful techniques. Firstly, in many species it is relatively easy to control encounter rates mating in the laboratory or in semi-natural field enclosures (see above for excellent examples with *Lacerta vivipara*). By directly manipulating female mating rates and combining with field tests with, for example, offspring survival, we can expect to understand the contexts in which indirect genetic effects are important. As advocated by most researchers in this field, carefully controlled breeding designs will also allow the crucial tests of the benefits of multiple mating from mating with several males (see extensive discussion in Slatyer *et al.* 2012). Researchers using lizard systems are yet to realize this potential as demonstrated by the fact that only one experimental study (LaDage *et al.* 2008) met the criteria for inclusion in the meta-analyses by Slatyer *et al.* (2012). In their recent meta-analysis across a broader range of taxa examining the genetic benefits of polyandry, Slatyer *et al.* (2012) found polyandry had a broadly beneficial effect on offspring fitness traits. The strength of this meta-analysis was that it was confined to studies using an experimental approach specifically designed to quantify the potential genetic effects after controlling for the number of matings of monandrous and polyandrous females, i.e., the rigorous experimental design of Tregenza and Weddell (1998) as exemplified, for example,

by Fisher *et al.* (2006). With carefully designed breeding experiments that control for genetic relatedness between partners it will also be possible to advance our understanding of the importance of “good genes” versus “compatible genes”, including whether their effects are context-dependent on levels of inbreeding-outbreeding.

Simmons (2005) emphasized that experimental protocols or taxa where the effects of maternal effects can be controlled (which can confound our analyses of genetic effects) are important. One key maternal effect that is often hard to control is maternal allocation to offspring (as discussed earlier). For example, larger females may attract more partners but also produce larger offspring. In lizards, separating out effects of offspring size from offspring quality led to the development of ‘allometric engineering’ techniques, allowing the experimenter to efficiently manipulate offspring size in both oviparous and viviparous species (Sinervo *et al.* 1992; Olsson *et al.* 2002). Thus far, this technique has not been used to examine size-dependence of indirect genetic effects but its potential is clear, especially when combined with release of offspring into the wild.

15.5.4 Greater understanding of costs of multiple mating for females (and males)

Understanding of costs of multiple mating for females (and males) is still poor for lizards which is one of the reasons for the current debate on the role that such costs play in the explaining polyandry. This is despite the important role that lizards (and snakes) have played in understanding costs of reproduction in general and the role that such costs play in explaining life history variation. We suggest increased attention examining costs associated with multiple mating (especially to females), especially those associated with the risk of injury, predation and/or disease will provide important insights and help resolve the contexts under which polyandry is favored (e.g., especially if combined with concurrent examination of the indirect genetic benefits). As discussed earlier, it is crucial we carefully (probably through experimental control initially) separate out costs associated with multiple mating with the same male versus mating with multiple males.

15.6 ACKNOWLEDGEMENTS

We thank Justin Rheubert, Dustin Siegel, Stanley Trauth, and Barrie Jamieson for inviting us to contribute to this publication. We would like to acknowledge the ongoing support of the Australian Research Council to our work. Jo McEvoy's assistance with literature searches and data extraction for the Table and Geoff While contributions to discussions and drafts of this chapter are gratefully acknowledged.

15.7 LITERATURE CITED

- Abell, A. J. 1997. Estimating paternity with spatial behaviour and DNA fingerprinting in the striped plateau lizard, *Sceloporus virgatus* (Phrynosomatidae). *Behavioral Ecology and Sociobiology* 41: 217–226.
- Akçay, E. and Roughgarden, J. 2007. Extra-pair paternity in birds: review of the genetic benefits. *Evolutionary Ecological Research* 9: 855–868.
- Alonzo, S. H. 2010. Social and coevolutionary feedbacks between mating and parental investment. *Trends in Ecology and Evolution* 25: 99–108.
- Alonzo, S. H. and Sinervo, B. 2001. Mate choice games, context-dependent good genes, and genetic cycles in the side-blotched lizard, *Uta stansburiana*. *Behavioral Ecology and Sociobiology* 49: 176–186.
- Ancona, S., Drummond, H. and Zaldivar-Rae, J. 2010. Male whiptail lizards adjust energetically costly mate guarding to male-male competition and female reproductive value. *Animal Behaviour* 79: 75–82.
- Andersson, M. 1994. *Sexual Selection*. Princeton University Press: New Jersey. pp. 519.
- Arnqvist, G. and Kirkpatrick, M. 2005. The evolution of infidelity in socially monogamous passerines: the strength of direct and indirect selection on extrapair copulation behavior in females. *The American Naturalist* 165: S26–S37.
- Arnqvist, G. and Nilsson, T. 2000. The evolution of polyandry: multiple mating and female fitness in insects. *Animal Behaviour* 60: 145–164.
- Arnqvist, G. and Rowe, L. 2005. *Sexual conflict*. Princeton University Press, New Jersey. pp. 330.
- Badyaev, A. V. and Qvarnstrom, A. 2002. Putting sexual traits into the context of an organism: a life-history perspective in studies of sexual selection. *Auk* 119: 301–310.
- Bateman, A. J. 1948. Intra-sexual selection in *Drosophila*. *Heredity* 2: 349–368.
- Bateson, Z. W., Krenz, J. D. and Sorensen, R. E. 2011. Multiple paternity in the common five-lines skink (*Plestiodon fasciatus*). *Journal of Herpetology* 45: 504–510.
- Berry, O. F. 2006. Inbreeding and promiscuity in the endangered grand skink. *Conservation Genetics* 7: 427–437.

- Birkhead, T. R. and Møller, A. P. 1998. Sperm competition, sexual selection and different routes to fitness. Pp 757-781. In Birkhead, T. R. and Møller, A. P. (eds), *Sperm Competition and Sexual Selection*. Academic Press: Cambridge.
- Birkhead, T. R. and Pizzari, T. 2002. Postcopulatory sexual selection. *Nature Reviews Genetics* 3: 262-273.
- Bleu, J., Bessa-Gomes, C. and Laloi, D. 2012. Evolution of female choosiness and mating frequency: effects of mating cost, density and sex ratio. *Animal Behaviour* 83: 131-136.
- Bonier, F., Eikenaar, C., Martin, P. R. and Moore, I. T. 2014. Extrapair paternity rates vary with latitude and elevation in Emberizid sparrows. *The American Naturalist* 183: 54-61.
- Botero, C. A. and Rubenstein, D. R. 2012. Fluctuating environments, sexual selection and the evolution of flexible mate choice in birds. *Plos One* 7: e32311.
- Bull, C. M., Cooper, S. J. B. and Baghurst, B. C. 1998. Social monogamy and extra-pair fertilization in an Australian lizard, *Tiliqua rugosa*. *Behavioral Ecology and Sociobiology* 44: 63-72.
- Bull, C. M., Godfrey, S. S. and Gordon, D. M. 2012. Social networks and the spread of Salmonella in a sleepy lizard population. *Molecular Ecology* 21: 4386-4392.
- Calsbeek, R. and Bonneaud, C. 2008. Postcopulatory fertilization bias as a form of cryptic sexual selection. *Evolution* 62: 1137-1148.
- Calsbeek, R. and Sinervo, B. 2002. Uncoupling direct and indirect components of female choice in the wild. *Proceedings of the National Academy of Sciences of the United States of America* 99: 14897-14902.
- Calsbeek, R. and Sinervo, B. 2004. Within clutch variation in offspring sex determined by differences in sire body size: cryptic mate choice in the wild. *Journal of Evolutionary Biology* 17: 464-470.
- Chapple, D. G. 2003. Ecology, life-history, and behavior in the Australian scincid genus *Egernia*, with comments on the evolution of complex sociality in lizards. *Herpetological Monographs* 17: 145-180.
- Chapple, D. G. and Keogh, J. S. 2005. Complex mating system and dispersal patterns in a social lizard, *Egernia whitii*. *Molecular Ecology* 14: 1215-1227.
- Cockburn, A., Legge, S. and Double, M. C. 2002. Sex ratios in birds and mammals: can the hypotheses be disentangled? Pp. 266-286. In I. C. W. Hardy (ed.), *Sex ratios: concepts and research methods*. University Press: Cambridge.
- Corl, A., Lancaster, L. T. and Sinervo, B. 2012. Rapid formation of reproductive isolation between two populations of side-blotched lizards, *Uta stansburiana*. *Copeia* 2012: 593-602.
- Cornwallis, C. K. and Uller, T. 2010. Towards an evolutionary ecology of sexual traits. *Trends in Ecology and Evolution* 25: 145-152.
- Cornwallis, C. K. West, S. A. Davis, K. E. and Griffin, A. S. 2010. Promiscuity and the evolutionary transition to complex societies. *Nature* 466: 969- U91.

- Doody, J. S., Burghardt, G. M. and Dinets, V. 2013. Breaking the social-non-social dichotomy: a role for reptiles in vertebrate social behavior research? *Ethology* 119: 95-103.
- Dubey, S., Chevalley, M. and Shine, R. 2011. Sexual dimorphism and sexual selection in a montane scincid lizard (*Eulamprus leuraensis*). *Austral Ecology* 36: 68-75.
- Eberhard, W. G. and Cordero, C. 2003. Sexual conflict and female choice. *Trends in Ecology and Evolution* 18: 438-439.
- Eizaguirre, C., Laloi, D., Massot, M., Richard, M., Federici, P. and Clobert, J. 2007. Condition dependence of reproductive strategy and the benefits of polyandry in a viviparous lizard. *Proceedings of the Royal Society of London B* 274: 425-430.
- Faria, C. M. A., Zarza, E., Reynoso, V. H. and Emerson, B. C. 2010. Predominance of single paternity in the black spiny-tailed iguana: conservation genetic concerns for female-biased hunting. *Conservation Genetics* 11: 1645-1652.
- Fedorka, K. M. and Mousseau, T. A. 2002. Material and genetic benefits of female multiple mating and polyandry. *Animal Behaviour* 64: 361-367.
- Fenner, A. L., Godfrey, S. S. and Bull, M. C. 2011. Using social networks to deduce whether residents or dispersers spread parasites in a lizard population. *Journal of Animal Ecology* 80: 835-843.
- Fisher, D. O., Double, M. C., Blomberg, S. P., Jennions, M. D. and Cockburn, A. 2006. Post-mating sexual selection increases lifetime fitness of polyandrous females in the wild. *Nature* 444: 89-92.
- Fitze, P. S., Le Galliard, J. F., Federici, P., Richard, M. and Clobert, J. 2005. Conflict over multiple-partner mating between males and females of the polygynandrous common lizards. *Evolution* 59: 2451-2459.
- Fitze, P. S., Cote, J. and Clobert, J. 2010. Mating order-dependent female mate choice in the polygynandrous common lizard *Lacerta vivipara*. *Oecologia* 162: 331-341.
- Garcia-Gonzalez, F. and Simmons, L. W. 2005. Sperm viability matters in insect sperm competition. *Current Biology* 15: 271-275.
- Gardner, M., Bull, C. M., Cooper, S. J. B. and Duffield, G. A. 2000. Microsatellite mutations in litters of the Australian lizard *Egernia stokesii*. *Journal of Evolutionary Biology* 13: 551-560.
- Gardner, M. G., Bull, C. M., Cooper, S. J. B. and Duffield, G. A. 2002. High levels of genetic monogamy in the social Australian lizard *Egernia stokesii*. *Molecular Ecology* 11: 1787-1794.
- Godfrey, S. S., Bull, C.M., James, R. and Murray, K. 2009. Network structure and parasite transmission in a group living lizard, *Egernia stokesii*. *Behavioral Ecology and Sociobiology* 63: 1045-1056.
- Godfrey, S. S., Moore, J. A., Nelson, N. J. and Bull, C. M. 2010. Social network structure and parasite infection patterns in a territorial reptile, the tuatara (*Sphenodon punctatus*). *International Journal for Parasitology* 40: 1575-1585.

- Griffin, A. S. Alonzo, S. H., and Cornwallis, C. K. 2013. Why do cuckolded males provide paternal care? *Plos Biology* 11: e1001520.
- Griffith, S., Owens, I. and Thuman, K. 2002. Extrapair paternity in birds: a review of interspecific variation and adaptive function. *Molecular Ecology* 11: 2195–2212.
- Gullberg, A., Olsson, M. and Tegelström, H. 1997 Male mating success, reproductive success and multiple paternity in a natural population of sand lizards: behavioural and molecular genetics data. *Molecular Ecology* 6: 105–112.
- Gwynne, D. T. 2008. Sexual conflict over nuptial gifts in insects. *Annual Review of Entomology* 53: 83-101.
- Hettyey, A., Hegyi, G., Puurtinen, M., Hoi, H., Torok, J. and Penn, D. J. 2010. Mate choice for genetic benefits: time to put the pieces together. *Ethology* 116: 1-9.
- Hewison, A. J. M. and Gaillard, J. M. 1999. Successful sons or advantaged daughters? The Trivers-Willard model and sex-biased maternal investment in ungulates. *Trends in Ecology and Evolution* 14: 229-234.
- Hofmann, S. and Henle, K. 2006. Male reproductive success and intrasexual selection in the common lizard determined by DNA microsatellites. *Journal of Herpetology* 40: 1–6.
- Holman, L. and Kokko, H. 2013. The consequences of polyandry for population viability, extinction risk and conservation . *Philosophical Transaction of the Royal Society of London B* 368: 20120053.
- Horvathova, T., Nakagawa, S. and Uller, T. 2012. Strategic female reproductive investment in response to male attractiveness in birds. *Proceedings of the Royal Society of London B* 279: 163-170.
- Hughes, W. O. H., Oldroyd, B. P., Beekman, M. and Ratnieks, F. L. W. 2008. Ancestral monogamy shows kin selection is key to the evolution of eusociality. *Science* 320: 1213-1216
- Jennions, M. D. and Petrie, M. 2000. Why do females mate multiply? A review of the genetic benefits. *Biological Reviews* 75: 21-64.
- Keogh, J. S., Umbers, K. D. L. Wilson, E., Stapley, J. and Whiting, M. J. 2013. Influence of alternate reproductive tactics and pre- and postcopulatory sexual selection on paternity and offspring performance in a lizard. *Behavioral Ecology and Sociobiology* 67: 629-638.
- Kokko, H. 1999. Cuckoldry and the stability of biparental care. *Ecology Letters* 2: 247-255.
- Komduer, J. and Pen, I. 2002. Adaptive sex allocation in birds: the complexities of linking theory and practice. *Philosophical Transaction of the Royal Society of London B* 357: 373-380.
- LaDage, L. D. Gutzke, W. H. N. Simmons, R. A., II and Ferkin, M.H. 2008. Multiple mating increases fecundity, fertility and relative clutch mass in the female leopard gecko (*Eublepharis macularius*). *Ethology* 114: 512-520.
- Laloi, D., Eizaguirre, C., Federici, P. and Massot, M. 2011. Female choice for heterozygous mates changes along successive matings in a lizard. *Behavioural Processes* 88: 149-154.

- Laloi, D., Richard, M., Federici, P., Clobert, J., Teillac-Deschamps, P. and Massot, M. 2009. Relationship between female mating strategy, litter success and offspring dispersal. *Ecology Letters* 12: 823–829.
- Laloi, D., Richard, M., Lecomte, J., Massot, M. and Clobert, J. 2004. Multiple paternity in clutches of common lizard *Lacerta vivipara*: data from microsatellite markers. *Molecular Ecology* 13: 719–723.
- Lebas, N. R. 2001. Microsatellite determination of male reproductive success in a natural population of the territorial ornate dragon lizard, *Ctenophorus ornatus*. *Molecular Ecology* 10: 193–203.
- Le Galliard, J.F., Fitze, P. S., Ferriere, R. and Clobert, J. 2005. Sex ratio bias, male aggression, and population collapse in lizards. *Proceedings of the National Academy of Sciences of the United States of America* 102: 18231–18236.
- Le Galliard, J. F. Cote, J. and Fitze, P. S. 2008. Lifetime and intergenerational fitness consequences of harmful male interactions for female lizards. *Ecology* 89: 56–64.
- Leu, S. T., Bashford, J., Kappeler, P. M. and Bull, C. M. 2010. Association networks reveal social organization in the sleepy lizard. *Animal Behaviour* 79: 217–225.
- Lopez, P., Aragon, P. and Martin, J. 2003. Responses of female lizards, *Lacerta monticola*, to males' chemical cues reflect their mating preference for older males. *Behavioral Ecology and Sociobiology* 55: 73–79.
- Lukas, D. and Clutton-Brock, T. H. 2013. The evolution of social monogamy in mammals. *Science* 341: 526–530.
- Madsen, T. 2008. Female nonavian reptiles benefit from multiple matings. *Molecular Ecology* 17: 3753–3753.
- Madsen, T. 2011. Cost of multiple matings in female adders (*Vipera berus*). *Evolution* 65: 1823–1825.
- Madsen, T., Shine, R., Loman, J. and Håkansson, T. 1992. Why do female adders copulate so frequently? *Nature* 355: 440–441.
- Madsen, T., Shine, R., Olsson, M. and Wittzell, H. 1999. Conservation biology: restoration of an inbred adder population. *Nature* 402: 34–35.
- Madsen, T. Ujvari, B. and Olsson, M. 2004. Novel genes continue to enhance population growth in adders (*Vipera berus*). *Biological Conservation* 120: 145–147.
- Martin, J. and Lopez, P. 2013. Responses of female rock lizards to multiple scent marks of males: effects of male age, male density and scent over-marking. *Behavioural Processes* 94: 109–114.
- Morrison, S., Keogh, S. and Scott, A. 2002. Molecular determination of paternity in a natural population of the multiply mating polygynous lizard *Eulamprus heatwolei*. *Molecular Ecology* 11: 535–545.
- Neff, B. D. and Pitcher, T. E. 2005. Genetic quality and sexual selection: an integrated framework for good genes and compatible genes. *Molecular Ecology* 14: 19–38.
- Neff, B. D. and Pitcher, T. E. 2008. Mate choice for non-additive genetic benefits: a resolution to the lek paradox. *Journal of Theoretical Biology* 254: 147–155.

- Noble, D. W. A., Keogh, J. S. and Whiting, M. J. 2013. Multiple mating in a lizard increases fecundity but provides no evidence for genetic benefits. *Behavioral Ecology* 24: 1128-1137.
- O'Connor, D. and Shine, R. 2004. Parental care protects against infanticide in the lizard *Egernia saxatilis* (Scincidae). *Animal Behaviour*. 68: 1361-1369.
- Oh, K. P. 2011. Inclusive fitness of 'kissing cousins': new evidence of a role for kin selection in the evolution of extra-pair mating in birds. *Molecular Ecology* 20: 2657-2659.
- Olsson, M. 2001. 'Voyeurism' prolongs copulation in the dragon lizard *Ctenophorus fordi*. *Behavioral Ecology and Sociobiology* 50: 378-381.
- Olsson, M. and Madsen, T. 1995. Female choice on male quantitative traits in lizards – why is it so rare? *Behavioral Ecology and Sociobiology* 36: 179-184.
- Olsson, M. and Madsen, T. 1996. Costs of mating with infertile males selects for late emergence in female sand lizards (*Lacerta agilis* L). *Copeia* 2: 462-464.
- Olsson, M. and Madsen, T. 1998. Sexual selection and sperm competition in reptiles. Pp 503-578. In T. R. Birkhead and A. P. Møller (eds), *Sperm Competition and Sexual Selection* Academic Press, Cambridge.
- Olsson, M. and Madsen, T. 2001. Promiscuity in sand lizards (*Lacerta agilis*) and adder snakes (*Vipera berus*): causes and consequences. *Journal of Heredity* 92: 190-197.
- Olsson, M. and Shine, R. 1997. Advantages of multiple matings to females: a test of the infertility hypothesis using lizards. *Evolution* 51: 1684-1688.
- Olsson, M. and Uller, T. 2009. On parsimonious paternity and scientific rigor: a reply to Madsen. *Molecular Ecology* 18: 25-27.
- Olsson, M., Gullberg, A., Tegelstrom, H., Madsen, T. and Shine, R. 1994a. Can female adders multiply. *Nature* 369: 528-528.
- Olsson, M., Madsen, T., Shine, R., Gullberg, A. and Tegelstrom, H. 1994b. Rewards of promiscuity – a reply. *Nature* 372: 230-230.
- Olsson, M., Shine, R., Madsen, T., Gullberg, A. and Tegelstrom, H. 1996. Sperm selection by females. *Nature* 383: 585-585.
- Olsson, M., Birkhead, T. and Shine, R. 1999. Can relaxed time constraints on sperm production eliminate protandry in an ectotherm? *Biological Journal of the Linnean Society* 66: 159-170.
- Olsson, M., Wapstra, E. and Olofsson, C. 2002. Offspring size-number strategies: experimental manipulations of offspring size in a viviparous lizard (*Lacerta vivipara*). *Functional Ecology* 16: 135-141.
- Olsson, M., Madsen, T., Nordby, J., Wapstra, E., Ujvari, B. and Wittsell, H. 2003. Major histocompatibility complex and mate choice in sand lizards. *Proceedings of the Royal Society of London B* 270: S254-S256.
- Olsson, M., Madsen, T., Ujvari, B. and Wapstra, E. 2004a. Fecundity and MHC affects ejaculation tactics and paternity bias in sand lizards. *Evolution* 58: 906-909.

- Olsson, M., Ujvari, B., Madsen, T., Uller, T. and Wapstra, E. 2004b. Haldane rules: costs of outbreeding at production of daughters in sand lizards. *Ecology Letters* 7: 924-928.
- Olsson, M., Madsen, T., Uller, T., Wapstra, E. and Ujvari, B. 2005a. The role of Haldane's rule in sex allocation. *Evolution* 59: 221-225.
- Olsson, M., Madsen, T., Wapstra, E., Silverin, B., Ujvari, B. and Wittsell, H. 2005b. MHC, health, colour, and reproductive success in sand lizards. *Behavioural Ecology and Sociobiology* 58: 289-294.
- Olsson, M., Ujvari, B., Wapstra, E., Madsen, T., Shine, R. and Bensch, S. 2005c. Does mate guarding prevent rival mating in snow skinks? A test using AFLP. *Herpetologica* 61: 389-394.
- Olsson, M., Healey, M., Wapstra, E., Schwartz, T., Lebas, N. and Uller, T. 2007. Mating system variation and morph fluctuations in a polymorphic lizard. *Molecular Ecology* 16: 5307-5315.
- Olsson, M., Schwartz, T., Wapstra, E., Uller, T., Ujvari, B., Madsen, T. and Shine, R. 2011a. Climate change, multiple paternity and offspring survival in lizards. *Evolution* 65: 3323-3326.
- Olsson, M., Wapstra, E., Schwartz, T., Madsen, T., Ujvari, B. and Uller, T. 2011b. In hot pursuit: fluctuating mating system and sexual selection in sand lizards. *Evolution* 65: 574-583.
- Oppliger, A., Degen, L., Bouteiller-Reuter, C. and John-Alder, H. B. 2007. Promiscuity and high level of multiple paternity in common wall lizards, *Podarcis muralis*: data from microsatellite markers. *Amphibia-Reptilia* 28: 301-303.
- Parker, G. A. and Birkhead, T. R. 2013. Polyandry: the history of a revolution. *Philosophical Transactions of the Royal Society of London B* 368: 20120335.
- Pizzari, T. and Wedell, N. 2013. Introduction: the polyandry revolution. *Philosophical Transactions of the Royal Society of London B* 368: 20120041.
- Pen, I., Uller, T., Feldmeyer, B., Harts, A., While, G. M. and Wapstra, E. 2010. Climate-driven population divergence in sex-determining systems. *Nature* 468: 436-U262.
- Price, T. A. R., Hurst, G. D. D. and Wedell, N. 2010. Polyandry prevents extinction. *Current Biology* 20: 471-475.
- Puurtinen, M., Ketola, T. and Kotiaho, J. S. 2009. The good-genes and compatible-genes benefits of mate choice. *The American Naturalist* 174: 741-752.
- Richard, M., Massot, M., Clobert, J. and Meylan, S. 2012. Litter quality and inflammatory response are dependent on mating strategy in a reptile. *Oecologia* 170: 39-46.
- Salvador, J., Diaz, J. A., Veija, J. P., Bloor, P. and Brown, R. P. 2008. Correlates of reproductive success in male lizards of the alpine species *Iberolacerta cyreni*. *Behavioral Ecology* 19: 169-176.
- Senar, J. C., Figuerola, J. and Pascual, J. 2002. Brighter yellow blue tits make better parents. *Proceedings of the Royal Society of London B* 269: 257-261.
- Sever, D. M. and Hamlett, W.C. 2002. Female sperm storage in reptiles. *Journal of Experimental Zoology* 292: 187-199.

- Sheldon, B. C. 1994. Male phenotype, fertility, and the pursuit of extra-pair copulations by female birds. *Proceedings of the Royal Society of London B* 257: 25–30.
- Sherman, C. D. H., Wapstra, E., Uller, T. and Olsson, M. 2008. Males with high genetic similarity to females sire more offspring in sperm competition in Peron's tree frog *Litoria peronii*. *Proceedings of the Royal Society of London B* 275: 971–978.
- Sherman, C. D. H., Wapstra, E. and Olsson, M. 2009. Consistent male-male paternity differences across female genotypes. *Biology Letters* 5: 232–234.
- Shine, R., Olsson, M. and Mason, R. T. 2000. Chastity belts in gartersnakes: the functional significance of mating plugs. *Biological Journal of the Linnean Society* 70: 377–390.
- Simmons, L. W. 2005. The evolution of polyandry: sperm competition, sperm selection, and offspring viability. *Annual Review of Ecology Evolution and Systematics* 36: 125–146.
- Sinervo, B., Dougherty, P., Huey, R. B. and Zamudio, K. 1992. Allometric engineering – a causal analysis of natural selection on offspring size. *Science* 258: 1927–1930.
- Sinervo, B., Calsbeek, R., Comendant, T., Both, C., Adamopoulou, C. and Clobert, J. 2006. Genetic and maternal determinants of effective dispersal: the effect of sire genotype and size at birth in side-blotched lizards. *The American Naturalist* 168: 88–89.
- Sinn, D. L., While, G. M. and Wapstra, E. 2008. Maternal care in a social lizard: links between female aggression and offspring fitness. *Animal Behaviour* 76: 1249–1257.
- Slatyer, R. A., Mautz, B. S., Backwell, P. R. Y. and Jennions, M. D. 2012. Estimating genetic benefits of polyandry from experimental studies: a meta-analysis. *Biological Reviews* 87: 1–33.
- Snook, R. R. 2005. Sperm in competition: not playing by the numbers. *Trends in Ecology and Evolution* 20: 46–53.
- Stapley, J., Hayes, C. M. and Keogh, J. S. 2003 Population genetic differentiation and multiple paternity determined by novel microsatellite markers from the Mountain Log Skink (*Pseudemoia entrecasteauxii*). *Molecular Ecology Notes* 3: 291–293.
- Stow, A. J. and Sunnucks, P. 2004. High mate and site fidelity in Cunningham's skinks (*Egernia cunninghami*) in natural and fragmented habitat. *Molecular Ecology* 13: 419–430.
- Tokarz, R. R. 1995. Mate choice in lizards – a review. *Herpetological Monographs* 9: 17–40.
- Tregenza, T. and Wedell, N. 1998. Benefits of multiple mates in the cricket *Gryllus bimaculatus*. *Ethology* 52: 1726–1730.
- Trivers, R. L. 1972. Parental investment and sexual selection. Pp. 136–179. In B Campbell (ed.), *Sexual selection and the descent of man, 1871–1971*. Aldine: Chicago.
- Uller, T. and Olsson, M. 2005. Multiple copulations in natural populations of lizards: evidence for the fertility assurance hypothesis. *Behaviour* 142: 45–56.
- Uller, T. and Olsson, M. 2008. Multiple paternity in reptiles: patterns and processes. *Molecular Ecology* 17: 2566–2580.

- Uller, T., While, G. M., Cadby, C. D., Harts, A., O'Connor, K., Pen, I. and Wapstra, E. 2011. Altitudinal divergence in maternal thermoregulatory behaviour may be driven by differences in selection on offspring survival in a viviparous lizard. *Evolution* 65: 2313-2324.
- Uller, T., Schwartz, T., Koglin, T. and Olsson, M. 2013. Sperm storage and sperm competition across ovarian cycles in the dragon lizard, *Ctenophorus fordi*. *Journal of Experimental Zoology Part A-Ecological Genetics and Physiology* 319: 404-408.
- Vahed, K. 1998. The function of nuptial feeding in insects: review of empirical studies. *Biological Reviews of the Cambridge Philosophical Society* 73: 43-78.
- Watson, P. J., Arnqvist, G. and Stallman, R. R. 1998. Sexual conflict and the energetic costs of mating and mate choice in water striders. *The American Naturalist* 151: 46-58.
- While, G. M. and Wapstra, E. 2009. Snow skinks (*Niveoscincus ocellatus*) do not shift their sex allocation patterns in response to mating history. *Behaviour* 146: 1405-1422.
- While, G. M., Uller, T. and Wapstra, E. 2009a. Within-population variation in social strategies characterize the social and mating system of an Australian lizard, *Egernia whitii*. *Austral Ecology* 34: 938-949.
- While, G. M., Uller, T. and Wapstra, E. 2009b. Family conflict and the evolution of sociality in reptiles. *Behavioral Ecology* 20: 245-250.
- While, G. M., Uller, T. and Wapstra, E. 2011. Variation in social organization influences the opportunity for sexual selection in a social lizard. *Molecular Ecology* 20: 844-852.
- While, G. M., Uller, T., Bordogna, G. and Wapstra, E. 2014. Promiscuity resolves constraints on social mate choice imposed by population viscosity. *Molecular Ecology* 23: 721-732.
- Wusterbarth, T. L., King, R. B., Duvall, M. R., Grayburn, W. S. and Burghardt, G. M. 2010. Phylogenetically widespread multiple paternity in new world natricine snakes. *Herpetological Conservation and Biology* 5: 86-93.
- Wedell, N., Gage, M. J. G. and Parker, G. A. 2002. Sperm competition, male prudence and sperm-limited females. *Trends in Ecology and Evolution* 17: 313-320.
- Yasui, Y. 1998. The 'genetic benefits' of female multiple mating reconsidered. *Trends in Ecology and Evolution* 13: 246-250.
- Zamudio, K. R. and Sinervo, E. 2000. Polygyny, mate-guarding, and posthumous fertilization as alternative male mating strategies. *Proceedings of the National Academy of Sciences of the United States of America* 97: 14427-14432.
- Zeh, J. A. and Zeh, D. W. 1996. The evolution of polyandry I: intragenomic conflict and genetic incompatibility. *Proceedings of the Royal Society of London B* 263: 1711-1717.
- Zeh, J. A. and Zeh, D. W. 2003. Toward a new sexual selection paradigm: polyandry, conflict and incompatibility (Invited article). *Ethology* 109: 929-950.