

# Parentage analyses suggest female promiscuity and a disadvantage for athletic males in the colour-polymorphic lizard *Podarcis melisellensis*

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**Abstract** Although laboratory measurements of whole-animal performance have become a standard tool in evolutionary biology, if and how interindividual variation in performance translates into differential fitness remains poorly understood. Particularly rare are studies that have connected performance to mating and reproductive success in the field. In this study, we use DNA microsatellite parentage analyses to study the fitness gradient in a colour-polymorphic lizard, *Podarcis melisellensis*. We report on two surprising findings. First, contrary to our expectations, individual sprint speed and bite force capacity correlated negatively, not positively, with male mating and reproductive success. Second, we found an unexpected degree of promiscuity in females. Also, contrary to traditional parental investment theory, the variation in

mating success and reproductive success was as high in females as in males. Our results call for a better integration of whole-animal performance and life history traits, and for a reconsideration of the ideas on the likeliness of sexual selection acting on female phenotypes.

**Keywords** Sexual selection · Whole-animal performance · Lacertidae · Microsatellites · Bateman's principle

## Introduction

A central tenet in evolutionary biology is that selection on discrete morphological, physiological or behavioural characteristics occurs through effects on whole-organism performance. The reasoning is that variation in functional performance capacity (the ability of the organism to accomplish ecologically relevant tasks such as feeding and locomotion) is likely to strongly correlate with variation in fitness components. A considerable number of studies have corroborated this idea by demonstrating that survival depends on integrated functions such as running ability (e.g. Jayne and Bennett 1990; Watkins 1996; O'Steen et al. 2002; Le Galliard et al. 2004; Miles 2004) and bite force capacity (Irschick and Meyers 2007). Fewer studies have explored the relationship between performance and reproductive success (Wilson et al. 2010).

Two lines of thought suggest that sexual selection, like natural selection, may target ecological performance traits (Lailvaux and Irschick 2006). First, a male's ability to acquire and maintain a territory and to fight off sexual rivals likely depends on integrated functions such as speed (Garland et al. 1990; Robson and Miles 2000), endurance (Lailvaux et al. 2005; Matsumasa and Murai 2005) and bite force (Lailvaux et al. 2004; Huyghe et al. 2005). Therefore, intrasexual selection is thought to promote these performance traits in males,

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especially males of territorial, polygynous species. Second, because females can base their mate choice decision on excellence in complex bodily functions leading to good health and resource holding potential, ecological performance can also be a target of female mate choice (e.g. Nicoletto 1991, 1993; Takahashi and Kohda 2004; Irschick et al. 2007).

Studies demonstrating sexual selection on performance traits are relatively rare (Lailvaux and Irschick 2006; Wilson et al. 2010), and many of them have settled with showing that performance is either correlated with the odds of winning rival fights, or is implicated in female choice. Yet, studying components of intra or intersexual selection in isolation may lead to erroneous conclusions on the adaptive nature of particular traits. The presumed positive relationship between reproductive output and performance might thus be too simplistic. The expression of any trait is linked with all other traits by energetic and structural trade-offs and greater investment in performance will affect the expression of other traits that also in turn affect reproduction. Life history theory shows us that we should not always expect greater expression of one trait—even performance—will increase reproductive output, rather it is an optimal balance (Wilson et al. 2010). For instance, a study by Stapley (2008) suggests that male competition in the mountain log skink *Pseudemoia entrecasteauxii* selects for orange ventral colour, indicative of dominance, whilst female choice targets an unrelated variable: courtship duration. Huyghe et al. (2012) demonstrated that in Dalmatian wall lizards, *Podarcis melisellensis*, males with high bite performance capacities are more likely to win fights with other males, but are rejected by females. In this respect, it seems wise to use reproductive success as a more inclusive yardstick when evaluating the importance of variation in performance traits, as it is likely to reflect effects of intra and intersexual (and also survival) selection.

In this study, we investigated the morphology-performance-fitness gradient (Arnold 1983) in the colour-polymorphic lizard *P. melisellensis*, by relating information on morphology (body size, shape, colour), sprint speed and bite force to reproductive output. Reproductive success of free-ranging males and females was estimated from parentage analyses. Next to a limited number of studies on other taxa (e.g. birds: Cramer 2013; arthropods: Hall et al. 2010; Nespolo et al. 2013), lizards have played an important role as model organisms in the morphology-performance-fitness research scheme, but only a limited number of studies have linked field reproductive success to phenotypic traits. In collared lizards (*Crotaphytus collaris*), males with higher sprint speeds sire more offspring (Husak and Fox 2006), because they were better able to defend the females in their territory (Husak et al. 2008). In the same species, high bite force is also favoured by females during mate choice events (Husak et al. 2009). Overall male activity (locomotion plus social interactions) also explained much of the variation in fertilization

success of male southern water skinks (*Eulamprus heatwolei*) in a large enclosure (Keogh et al. 2012).

Although in the last decade many authors have frequently argued otherwise, it is still widely believed that sexual selection is more intense in males than in females. This idea is primarily based on the Bateman's principle', i.e. the observation that in many species the variance of reproductive success is greater in males than in females (Bateman 1948). According to the parental investment theory (Trivers 1972), males experience relatively few costs per fertilization attempt, and therefore will increase their fecundity by mating with multiple partners. In contrast, females typically invest much more per reproductive event and therefore their strategy should be to mate in a very selective manner, i.e. only with high quality partners. Under this reasoning, the benefits of repeated matings to reproductive success are predicted to be smaller in females than in males. The Bateman principle has been criticised on several accounts (Dewsbury 2005; Tang-Martinez and Ryder 2005; Gowaty et al. 2012). First, in many species, male gamete production is not as inexpensive and unlimited as originally thought. For instance, male adders (*Vipera berus*) lose mass when building up sperm supplies (Olsson et al. 1997). In addition, sperm depletion as a result of multiple matings has been reported in diverse taxa (review in Wedell et al. 2002), including lizards (Olsson et al. 2004). These findings have eroded the thinking of males as the more 'eager' sex and have prompted studies on male mate selection (see Olsson 1993; Orrell and Jenssen 2002; Swierk et al. 2013 for examples concerning lizards). Second, females may actively solicit matings with multiple males (Madsen et al. 1992; Olsson and Madsen 1994), possibly to renew depleted sperm supplies, to promote sperm competition or cryptic female choice or for increased access to resources. These observations have challenged the image of females as the 'coy' sex.

Because they produce direct estimates of mating and reproductive success, parentage analyses provide a means of testing the idea that sexual selection is more intense in males than in females (Gopurenko et al. 2007). Therefore, this study uses parent-offspring multilocus microsatellite genotyping in a field population of *P. melisellensis* to (1) determine parentage and to (2) compare the variance in mating and reproductive success and the relationship between these two variables between males and females.

## Materials and methods

### Study species and locality

*P. melisellensis* is a medium-sized lacertid lizard occurring along the Adriatic coast and on islands in the Adriatic Sea. Populations of *P. melisellensis* vary in their degree of colour polymorphism as populations may consist of one, two or three

colour phenotypes (KH pers. obs.). At the study site on the island of Lastovo (Adriatic Sea, Croatia, N 42° 45' 38", E 16° 52' 55.2"), lizards have a white, yellow or orange ventral colour. The three morphs are distributed randomly and share the same microhabitat (Huyghe et al. 2007). During the mating season, but also throughout much of the activity season, males defend territories and readily engage in fights with intruders (Böhme 1981; Huyghe et al. 2012). Several females are typically found in a male's territory (KH pers. obs.).

#### Field sampling

The study site was an abandoned olive grove (150 m<sup>2</sup>). During three fieldtrips in 2006 (April, June and August), we captured adult and juvenile lizards by noose. To avoid recapture, each adult lizard was permanently marked by toe clipping. Tail tips ( $\pm 5$  mm) were stored in 95 % alcohol and used as sources of DNA. No new adults or juveniles were caught on the last day of each sampling event, suggesting that most resident individuals had been caught.

#### DNA microsatellite genotyping

For DNA microsatellite genotyping, we used the protocols described by Huyghe et al. (2010). Specimens were included in the analyses if they could be genotyped for at least eight out of 13 microsatellite loci (Huyghe et al. 2009). Genotypes of adult males ( $N=118$ ) and females ( $N=113$ ), captured during the first two field trips (April and June) were taken from Huyghe et al. (2010). All juvenile genotypes ( $N=220$ ) were assessed in the current study.

#### Population genetic and parentage analyses

To assess goodness of fit to Hardy-Weinberg equilibrium (HWE), we used the Markov chain method implemented in Genepop v3.3 (dememorization=1,000, batches=100, iterations per batch=1,000). Hatchlings were assigned to putative parents based on their multilocus genotype probabilities using Cervus v3.0.3 (Marshall et al. 1998) with minimum 80 % confidence level. Throughout, alpha values were corrected for multiple test biases with the sequential Bonferroni procedure.

#### Phenotypic traits

We have information on body length, head length, head height, head width, fore and hindlimb length, maximal bite force capacity and maximal sprint speed capacity for 47 adult males that were genotyped. These morphological and performance measures were taken from an earlier study in this population (see Huyghe et al. 2009 for the methodology used).

#### Mating patterns and sexual selection

To test two key assumptions of the Bateman principle, we calculated means and variances of mating and reproductive success for each sex. Absolute variances were standardized (variance $\times$ mean<sup>-2</sup>) in each sex to assess the opportunity for selection ( $I_{RS}$ ) and the opportunity for sexual selection ( $I_{MS}$ ). Bateman curves (i.e. linear regression of reproductive success against mating success) were constructed for each sex and compared using analysis of covariance.

#### Statistical analyses

All quantitative phenotypic data met the assumptions of normal distributions. A generalized linear model was used to assess the relationships between phenotypic traits and the number of offspring a male sired. This dependent variable followed a Poisson distribution. We included ventral colour as a factorial trait and body size, head size, fore limb length, hind limb length, maximal bite force capacity and maximal sprint speed capacity as covariates. We used principal component analysis (PCA) to obtain a single composite measure describing overall head dimensions ('head size'). The PCA resulted in a single new variable that explained 90.31 % of the variation in head length, width and height. Scores on this axis correlated strongly with all three head measures (all  $r>0.95$ ). Pearson correlation coefficients assessed the correlation between number of offspring and number of mates in both sexes.

#### Results

The overall genetic diversity (Table 1) in the study population was similar to that reported by Huyghe et al. (2009, 2010), except for loci Pmeli15 and Pmeli16, which now show significant HWE deviations. All significant HWE deviations involved heterozygote deficiencies. Compared to Huyghe et al. (2009), the numbers of alleles increased for all loci (average increase=17) in the present study.

Of 220 offspring genotyped, 87 % were assigned to a father, and 80 % to a mother. Seventy-one percent were assigned both parents. Multiple paternity was found in 85 % of the clutches. The body size of the smallest male siring was considered the minimal reproductive size (46.49 mm). Five smaller males were removed from all further statistical analyses. For 47 out of the remaining 113 genotyped males, we have all phenotypic data.

In both sexes, the number of mates varied considerably, ranging from 0 to 10 in males and from 0 to 12 in females (Fig. 1). The standardized variance of mating success ( $I_{MS}$ ) did not differ significantly between the sexes (males, 3.15; females, 3.35;  $F_{118,112}=1.003$ ,  $P=0.49$ ). The number of

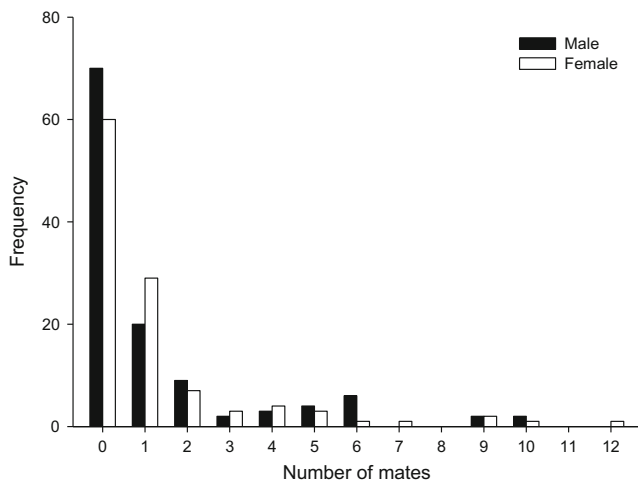
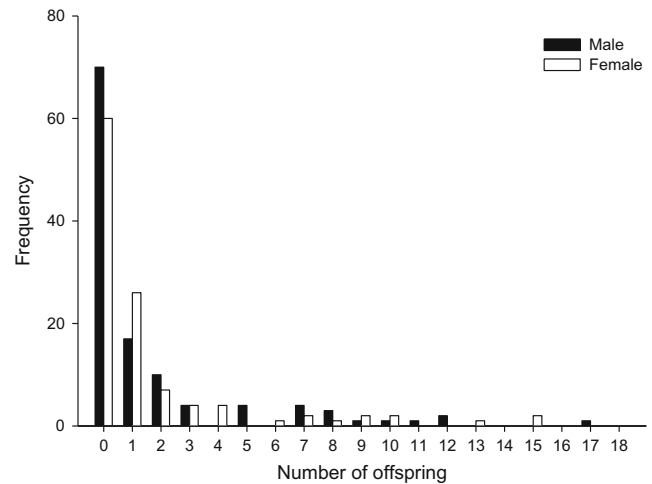
**Table 1** Overall genetic diversity of the population

Locus	N	N <sub>A</sub>	F <sub>IS</sub>	P
Pmeli-02	444	49	0.112	<i>&lt;0.001</i>
Pmeli-04	420	46	0.199	<i>&lt;0.001</i>
Pmeli-05	450	39	-0.0001	0.386
Pmeli-07	410	32	0.102	<i>&lt;0.001</i>
Pmeli-08	426	56	0.003	0.317
Pmeli-10	453	28	0.013	0.722
Pmeli-11	446	34	0.016	0.074
Pmeli-13	418	27	0.012	0.359
Pmeli-14	452	47	0.027	0.007
Pmeli-15	453	30	0.008	<i>&lt;0.001</i>
Pmeli-16	450	42	0.085	<i>&lt;0.001</i>
Pmeli-18	404	41	0.229	<i>&lt;0.001</i>
Pmeli-19	433	64	0.156	<i>&lt;0.001</i>

Significant *P* values after sequential Bonferroni correction are in italic  
*N* number of individuals, *N<sub>A</sub>* number of alleles

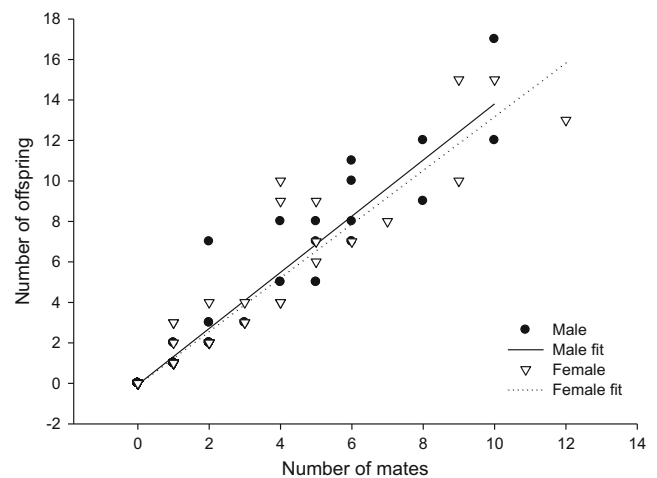
offspring produced over the total sampling period also varied considerably, between 0 to 17 in males and 0 to 15 in females (Fig. 2). The opportunity for selection (*I<sub>RS</sub>*, the standardized variance of reproductive success) did not differ between sexes (males, 3.70; females, 3.80;  $F_{118,112}=1.033$ ,  $P=0.43$ ). In both sexes, the number of offspring sired correlated strongly with mating success (males:  $r^2=0.90$ ; females:  $r^2=0.99$ ). Bateman's curves for males and females were very similar (Fig. 3); slopes of linear regressions relating number of offspring and number of mates did not differ between the sexes (ANCOVA,  $F_{1,226}=0.027$ ,  $P=0.87$ ).

Our effort to predict male mating success (the number of females with which males produced offspring) from

**Fig. 1** Histogram of the number of mates that were found through microsatellite parentage analyses for male (black) and female (white) *P. melisellensis***Fig. 2** Histogram of the number of offspring that were assigned through microsatellite parentage analyses to male (black) and female (white) *P. melisellensis*

phenotypic characteristics (morphometrics, colour, physiological performance) resulted in a significant model (likelihood ratio  $\chi^2_8=24.50$ ,  $P=0.002$ , Table 2) that contained sprint speed (Wald  $\chi^2=5.23$ ,  $P=0.02$ ) and maximal bite force capacity (Wald  $\chi^2=6.89$ ,  $P=0.009$ ) as the sole predictive variables. Surprisingly, males with lower maximal sprint speeds and lower maximal bite force capacities successfully mated with more females than males with higher values for these performance traits ( $\beta=-0.006$  and  $\beta=-0.20$ , respectively).

A similar analysis on male reproductive success (number of offspring sired) resulted in a significant model (likelihood ratio  $\chi^2_8=29.31$ ,  $P<0.001$ , Table 3) in which ventral colour (Wald  $\chi^2=10.23$ ,  $P=0.006$ ), maximal sprint speed capacity (Wald  $\chi^2=9.76$ ,  $P=0.002$ ) and maximal bite force capacity (Wald  $\chi^2=7.00$ ,  $P=0.008$ ) explained a significant part of the

**Fig. 3** Bateman's gradients showing the relation between number of mates (*x*-axis) and number of offspring (*y*-axis) for male (black) and female (white) *P. melisellensis*; Lines represent linear regression lines

**Table 2** Results of the generalized linear model analysis with number of offspring as dependent variable

Trait	Wald $\chi^2$	$\beta$	<i>P</i>
Colour	10.23		<i>0.006</i>
Body length	0.053	0.014	0.82
Head size	0.048	-0.063	0.83
Bite force capacity	7.00	-0.172	<i>0.008</i>
Hind limb length	2.73	0.103	0.10
Fore limb length	1.19	0.101	0.27
Sprint speed capacity	9.76	-0.007	<i>0.002</i>

Significant values are shown in italic

variation. Controlling for all other variables, orange males produced more offspring than yellow males. The reproductive success of white males was intermediate and not statistically different from the two other colour morphs. The negative effect of elevated physiological performance on mating success is reflected in a similar outcome for reproductive success. Just as for the effects on mating success, males with lower maximal sprint speed and lower maximal bite force capacities produced more offspring than males with higher values for these performance traits ( $\beta = -0.007$  and  $\beta = -0.17$  respectively). None of the morphometric traits (body and head size, fore and hindlimb length) had a significant role in the model.

## Discussion

Our field study of reproductive success in an island population of the lizard *P. melisellensis* has resulted in two unexpected findings (albeit to varying degrees). First, the variances in mating success and reproductive success were equally high for females and males. This observation is at odds with Bateman's principle, but corroborates recent studies suggesting that in some species, sexual selection may be just as intense in females as it is in males. Second, we found that

**Table 3** Results of the generalized linear model analysis with number of female mates as dependent variable

Trait	Wald $\chi^2$	$\beta$	<i>P</i>
Colour	5.28		0.07
Body size	0.20	-0.037	0.65
Head size	0.01	0.042	0.92
Bite force capacity	6.89	-0.20	<i>0.009</i>
Hind limb length	3.55	0.15	0.06
Fore limb length	1.05	0.12	0.31
Sprint speed capacity	5.23	-0.006	<i>0.022</i>

Significant values are shown in italic

male mating success and reproductive success correlated negatively with measures of whole-animal performance, such that males that excelled in maximal sprint speed and bite force capacity sired relatively fewer offspring.

## Female sexual selection?

We found a considerable degree of promiscuity in our study population. Many males and females produced offspring with several partners within a single activity season. A tendency to mate with multiple females is generally expected in males, especially in species like *P. melisellensis* that lack parental care. Our observation that females also have high numbers of sexual partners is a more challenging issue. Indeed, until recently, it was widely assumed that female reproductive success is limited by parental involvement, not by the number of mates acquired (Bateman 1948; Trivers 1972; Wade and Shuster 2002). In addition, mating itself is costly to females in many animals (e.g. Watson et al. 1998; Crudginton and Siva-Jothy 2000), including lizards (Olsson 1995; Fitze et al. 2005; Le Galliard et al. 2008; McLean and Stuart-Fox 2010; McLean et al. 2010; White et al. 2011). Thus theoretically, females should be less inclined to mate multiply than males, yet, a growing number of empirical studies, like ours, have refuted this prediction, and three types of hypotheses have been put forward to explain female promiscuity.

First, females may derive benefits from mating with different males, if males contribute to egg production or offspring survival. It is unlikely that this is the case for *P. melisellensis* (and most other lizard species), because males do not provide parental care. Moreover, there is neither evidence that male lizards produce ejaculates containing substances that contribute to female reproductive resources (Depeiges et al. 1987; Uller and Olsson 2008), nor that they provide other kinds of 'nuptial gifts' (such as food or nesting material, e.g. Vahed 1998; Tryanowski and Hromada 2005). Hence, a more likely possibility is that by mating with multiple males, the female increases the chance that all of her eggs will be fertilized. This may be important if males provide sperm that is of low quality or in small quantities, or when the fertilization of successive clutches requires copious amounts of sperm. It is not clear how often such conditions apply for reptiles. Female sand lizards (*Lacerta agilis*) risk being left with infertile (immature) sperm when they only mate with males early in the season (Olsson and Madsen 1996). Sperm depletion is typically expected in 'solitary' animals, in which male–female encounter rates are low. This seems an unlikely condition for most lizards, which tend to live in high densities, especially in the mating season (Uller and Olsson 2008). It is certainly not the case in our study population. Gist and Congdon (1998) have argued that repeated mating in turtles may be necessary because sperm retained in the oviduct might be pushed out by the eggs, leaving few sperm cells to fertilize subsequent

clutches. We do not know whether *P. melisellensis* is capable of storing sperm across successive clutches. Many other lizard species do (e.g. Wapstra et al. 1999; Zamudio and Sinervo 2000; Calsbeek et al. 2007; Olsson et al. 2007). Nevertheless, Pellitteri-Rosa et al. (2012) demonstrated that female *Podarcis muralis* (a species closely related to *P. melisellensis*) cannot store sperm and, therefore, must copulate with at least one male in between consecutive clutches to have all eggs fertilized.

According to a second series of explanations, multiple mating provides females with indirect, genetic benefits. In the ‘trade-up’ hypothesis, females will mate with a subsequent male whenever they judge him of higher quality than their earlier partners. Female trade-up strategy has been reported in arthropods (Watson 1991; Bateman et al. 2001), fish (Bakker and Milinski 1991; Pitcher et al. 2003) and newts (Gabor and Halliday 1997). Direct evidence for its existence in reptiles is rare (Uller and Olsson 2008), but Laloï et al. (2011) found that female common lizards (*Zootoca vivipara*) become more selective during successive mating opportunities; they will mate indiscriminately with any male at the beginning of the mating season, but prefer males with higher levels of heterozygosity in subsequent encounters.

Multiple mating may also provide genetic benefits to females by facilitating sperm competition. In lizards, as in many other animals, selection on male fertilization success has resulted in the evolution of male traits such as copulatory plugs (e.g. in den Bosch 1994; Mayer and Arribas 2003; Moreira et al. 2007) and structures and behaviours to remove them (e.g. Moreira and Birkhead 2004), ornamented hemipenes that may help extend copulation duration (Olsson and Madsen 1998) and postcopulatory mate-guarding behaviour (e.g. Olsson 1995; Ancona et al. 2010). If sperm competitiveness is heritable, or if males with competitive sperm are of high general quality, females may benefit from multiple matings by setting up sperm ‘contests’ inside their reproductive tract. We must add that these assumptions have not yet been tested in reptiles.

A third way in which multiple mating may provide genetic benefits to females is by enhancing opportunities for cryptic female choice. According to this popular hypothesis, females mate multiply so that they can actively choose among ejaculates to increase offspring genetic quality or compatibility (see Olsson and Madsen 1998, 2001 for a review of studies on reptiles).

One problem with the forementioned ‘good-genes’ hypotheses is that they predict that fertilization success should be heavily biased towards the male (with the ‘best’ genes). This seems to be in conflict with the high degree of multiple paternity reported. Recent studies have found that the extent of multiple paternity in lizards varies widely among species, the percentage of clutches containing offspring of different fathers varying from less than 3 % in the Australian skink

*Egernia cunninghami* (Stow and Sunnucks 2004) up to 94 % in another Australian skink species, *Niveoscincus ocellatus* (Wapstra unpublished in Uller and Olsson 2008). With 85 %, *P. melisellensis* would be on the promiscuous side of this continuum. However, our estimate of multiple paternity cannot be compared directly to that of other studies, because it approximates the number of mates with which a female has at least one offspring over an entire activity season (several clutches), not the number of fathers siring offspring within one clutch. Still, it seems safe to assume that many females mate with several males within a reproductive cycle, which creates possibilities for sperm competition and cryptic female choice.

A fourth condition in which females may incur genetic benefits from multiple mating is when an unpredictable environment necessitates a genetically varied (i.e. multisired) offspring. Although theoretically sound (and not jeopardized by high levels of multiple paternity), this idea of ‘genetic bet-hedging’ is notoriously difficult to test in the field and its importance in reptilians is unknown (Uller and Olsson 2008).

The steep relationship between mating success and reproductive success in female *P. melisellensis* creates opportunities for sexual selection to act on female characteristics. Primarily due to the dominance of Bateman’s principle, sexual selection is traditionally considered to act more strongly on males than on females. However, the growing evidence that mating costs for males may be considerable (see Censky 1995; Cooper 1999; Ancona et al. 2010 for examples on lizards), suggests that males of some species should be quite careful in their selection of females, thereby opening the door for sexual selection acting on particular female phenotypes (Clutton-Brock 2009). Accordingly, males in some species of lizards are choosy. For instance, male *L. agilis* prefer to associate with larger females (Olsson 1993), male *Ctenophorus ornatus* prefer females with high throat UV chroma (LeBas and Marshall 2000) and male *Anolis carolinensis* favour unfamiliar females (Orrell and Jenssen 2002). In species where females compete for access to males, breeding territories or other resources necessary for offspring production, there may also be a role for intrasexual selection among females (Clutton-Brock 2009), but the importance of female-female combat remains largely unexplored in lizards and other reptiles (While et al. 2008). Alas, for *P. melisellensis*, we currently have little direct information on the costs of mating for males, their preferences for particular females or the significance of female-female combat (we have seen females fighting occasionally in the field), but the results of this study encourage further study into these topics.

#### Male performance, mating and reproductive success

A second unexpected finding of this study was that male mating and reproductive success correlated negatively with

two measures of whole-animal performance: bite force and sprint speed. As they should be better in defending territories (Garland et al. 1990; Robson and Miles 2000; Lailvaux et al. 2004; Huyghe et al. 2005; Husak et al. 2008) and more attractive to females (Nicoletto 1991, 1993; Takahashi and Kohda 2004; Husak et al. 2009), we expected that males with superior performance would sire more offspring, not less.

Several authors have noted that the particularities of the fitness gradient are still not completely understood. Too few studies have assessed the consequences of performance variation for survival in the field and hardly any have considered the effects on reproductive output. Studies that did examine putative fitness gradients demonstrated that the link between performance and fitness may depend on environmental conditions (e.g. resource availability, Le Galliard et al. 2004). Since our study was restricted to one activity season, we cannot assess the variability of the fitness gradient. One interesting possibility is that the association between particular performance traits and reproductive success changes depending on the relative success of certain male or female phenotypes—success that may be negatively frequency-dependent. For instance, in years where territorial males are successful, speed and bite force may correlate positively with reproductive success. However, negative frequency-dependent selection may render sneaker males more successful in the year thereafter, and speed and bite force would then exhibit no or even a negative correlation with reproductive output. In *P. melisellensis*, both male and female individuals belong to one of three morphs that differ in ventral colouration. Orange males bite harder and are dominant over white and yellow males, suggesting that they may constitute the ‘territorial’ morph. However, we currently do not have detailed information on the behaviour and reproductive strategies of these male and female colour morphs and, therefore, we cannot establish whether they are involved in evolutionary cycles such as described for the side-blotched lizard *Uta stansburiana* (Alonzo and Sinervo 2000; Sinervo et al. 2000).

Alternatively, our expectation that superior sprinting and bite force capacities should enhance reproductive output in males may simply be unwarranted. Perhaps we have focused on the wrong performance variable(s). In some species of lizards, resource holding potential was found to depend on endurance capacity, or the ability to remain active for a long period of time, rather than on sprint speed (Lailvaux et al. 2005; Salvador et al. 2008; Keogh et al. 2012). Because they require different proportions of fast, powerful muscle fibres to slow more fatigue-resistant fibres, endurance capacity and sprint speed are considered an antagonistic pair in vertebrate locomotor physiology (Bennett et al. 1984; Garland 1988; Vanhooydonck et al. 2014). If high endurance capacity enhances reproductive success, but is negatively correlated with low sprint speed, this might explain the negative relationship between reproductive output and sprint speed. It should be

noted, however, that most empirical studies have failed to confirm intraspecific conflicts between speed and endurance (Wilson et al. 2002; but see Herrel and Bonneaud 2012). A similar reasoning could be used to explain the negative effect of bite force on reproductive output, but here it is more difficult to establish an antagonistic variable.

One could also argue that speed and bite force are primarily relevant in the context of male-male combat (Garland et al. 1990; Robson and Miles 2000; Lailvaux et al. 2004; Huyghe et al. 2005). Perhaps we are misjudging the relative importance of male-male combat and female choice. Several recent studies have demonstrated that these two components of sexual selection may target different characteristics, or can affect the same characteristic in opposite ways. For instance, in mountain log skinks, *P. entrecasteauxii*, male competition favours orange ventral colour, whilst female choice favours courtship duration (Stapley 2008). In *P. melisellensis*, bite force is a decisive factor in male-male combat, but females prefer males with relatively poor bite force capacity (Huyghe et al. 2012). In the common lizard, *Z. vivipara*, males with lower bite force also get prior access to mating partners (Huyghe et al. 2013). It is unclear what causes females of these species to shy away from males that bite hard. Perhaps male fighting ability does not reflect male quality (Qvarnström and Forsgren 1998); perhaps females are just trying to avoid the physical damage of fierce mating bites. This type of explanation requires that female choice overrules the selective effects of male-male combat. This assumption may seem unlikely in the traditional view of lizard mating systems, in which the intrasexual component is deemed much more important than the intersexual one (Olsson and Madsen 1994, 1998). However, there is increasing evidence that female choice in lizards may be more important than previously thought (e.g. Martín and López 2000; Vitousek et al. 2007; Laloï et al. 2011).

In conclusion, the use of molecular parentage analyses in the colour-polymorphic lizard *P. melisellensis* has resulted in a number of unexpected findings that add to the growing call for a careful reappraisal for a number of ‘established’ ideas on the nature of the morphology-performance-fitness gradient, the roles and interactions of inter and intrasexual selection and the role of sexual selection in shaping the female phenotype.

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**Ethical standards** The authors declare that all experiments comply with the current laws of the country in which they were performed (Belgium).

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