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# Flat lizard female mimics use sexual deception in visual but not chemical signals

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Understanding what constrains signalling and maintains signal honesty is a central theme in animal communication. Clear cases of dishonest signalling, and the conditions under which they are used, represent an important avenue for improved understanding of animal communication systems. Female mimicry, when certain males take on the appearance of females, is most commonly a male alternative reproductive tactic that is condition-dependent. A number of adaptive explanations for female mimicry have been proposed including avoiding the costs of aggression, gaining an advantage in combat, sneaking copulations with females on the territories of other males, gaining physiological benefits and minimizing the risk of predation. Previous studies of female mimicry have focused on a single mode of communication, although most animals communicate using multiple signals. Male *Augrabies* flat lizards adopt alternative reproductive tactics in which some males (she-males) mimic the visual appearance of females. We experimentally tested in a wild population whether she-males are able to mimic females using both visual and chemical signals. We tested chemical recognition in the field by removing scent and relabelling females and she-males with either male or female scent. At a distance, typical males (he-males) could not distinguish she-males from females using visual signals, but during close encounters, he-males correctly determined the gender of she-males using chemical signals. She-males are therefore able to deceive he-males using visual but not chemical signals. To effectively deceive he-males, she-males avoid close contact with he-males during which chemical cues would reveal their deceit. This strategy is probably adaptive, because he-males are aggressive and territorial; by mimicking females, she-males are able to move about freely and gain access to females on the territories of resident males.

**Keywords:** female mimicry; multiple signals; lizard; chemical signal; visual signal; signal deception

## 1. INTRODUCTION

Classical sexual selection systems, where males are elaborately ornamented and territorial, are characterized by intense male rivalry (Andersson 1994; Andersson & Iwasa 1996). In these systems, fighting may be costly and individuals are at risk of physical injury (Clutton-Brock *et al.* 1979). For young males with little fighting experience, the risk of injury may be high because the disparity in fighting ability with older and larger males is often substantial (Cooper & Vitt 1987). One solution is to adopt an alternative reproductive tactic (Gross 1996) such as being a non-territorial ‘floater’, which reduces conflict with rival territorial males (Sinervo & Lively 1996), or to mask their true identity, such as in the case of female mimicry (Burley 1982; Slagsvold & Saetre 1991; Saetre & Slagsvold 1996; Sinervo & Lively 1996; Shine *et al.* 2001). Female mimicry takes many different forms, but can simply involve delaying maturation and retaining a female-like appearance until an individual is better able to deal with rival aggression (Martin & Forsman 1999). For example, some male birds delay plumage maturation to avoid harassment from aggressive rival males or because it

gives them a competitive advantage in contests (Saetre & Slagsvold 1996), while the lizard *Psammotromus algirus* delays the development of head colour, which would normally invite attack from other males (Martin & Forsman 1999). By mimicking a female, males are often able to gain access to females that are guarded by a resident male or on his territory (Dominey 1980; Zamudio & Sinervo 2000; Hanlon *et al.* 2005). Deceptive signalling may therefore have the dual role of reducing directed aggression or harassment and allowing access to females that may reside on a resident male’s territory.

Although the proximate function of a signal is to manipulate a receiver, signalling systems are thought to break down if, on average, signals are not honest (Maynard Smith & Harper 2003). How signals are constrained and how cheating is prevented is a central theme in animal communication and has attracted considerable recent attention (Johnstone 1995*a,b*; Zahavi & Zahavi 1997; Maynard Smith & Harper 2003; Whiting *et al.* 2003). We now have a relatively extensive list of examples of honest signals, verified through experimental manipulation of the signal. For example, threat posturing in side-blotched lizards is energetically expensive and can only be maintained by individuals in good condition (Brandt 2003). Our understanding of dishonest signals is also growing (e.g. Adams & Caldwell 1990; Møller 1990; Backwell *et al.* 2000;

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Hughes 2000; Briffa 2006). In the context of sexual selection, female mimicry dishonestly signals gender and can be adaptive for a certain class of males (Peschke 1987; Shine *et al.* 2001; Hanlon *et al.* 2005). One of the most spectacular examples of female mimicry occurs in the giant Australian cuttlefish *sepia apama*. Male giant cuttlefish are able to instantaneously mimic female colour, posture and behaviour, using neural control, at a rate of change of approximately 10 times per 15 min (Hanlon *et al.* 2005). While most examples of female mimicry involve visual signals, chemical mimicry of females by males can also occur (Mason & Crews 1985; Peschke 1987; Forsyth & Alcock 1990). Some male garter snakes *Thamnophis sirtalis parietalis* mimic female skin lipids (Mason & Crews 1985; Shine *et al.* 2000) when they emerge from hibernation, which attracts misdirected courtship from other males. This mimicry allows she-males to heat up faster in mating balls and protects them from avian predators, but its benefits are short-lived; typically, she-males only mimic female pheromones for a few days after emergence from hibernation (Shine *et al.* 2001). Therefore, the traditional hypothesis that female mimicry is sexually selected is not supported for garter snakes.

Because signal efficacy depends on both the signalling environment and the receiver's sensory system (Endler 1992, 1993; Johnstone 1997), most animals use multiple signals that may be of a visual, chemical or auditory nature (Hughes 1996; Rowe 1999; Maynard Smith & Harper 2003). For example, in lizards, visual signals are thought to be important at a distance while chemical signals are more important during close encounters (Lopez & Martin 2001; Lopez *et al.* 2002). Chemical and visual signals can also interact in a more complex way such that certain species that have less elaborate coloration may be more prone to using chemical signals (Hews & Benard 2001). While female mimicry of visual signals and/or behaviour has been documented for a number of lizard species (Cooper & Greenberg 1992; Wikelski *et al.* 1996; Zamudio & Sinervo 2000), chemical mimicry is largely unknown, the garter snake *T. s. parietalis* notwithstanding (Mason & Crews 1985; Shine *et al.* 2000). In garter snakes, males use both visual and chemical signals to select mates (Shine & Mason 2001). Recent reviews of signalling have emphasized the importance of understanding the role of multiple signals in animal communication and, in particular, how receivers deal with multiple signals (Johnstone 1995*a*, 1996, 1997; Rowe 1999; Andersson *et al.* 2002). While several studies have examined the mimicry of a single type of signal, we know of no study that has directly tested whether a single species is capable of producing multiple dishonest signals and how these signals may interact in the context of sexual selection.

Augrabies flat lizards (*Platysaurus broadleyi*) present a good system for examining the role of deceptive signalling because some adult males retain a female-like appearance and delay the onset of adult male coloration, even though they are sexually mature. Furthermore, they use multiple signals in a social context (M. J. Whiting 1995, personal observation) and adopt male alternative reproductive tactics (Whiting *et al.* 2006). At a distance, males use visual signals to evaluate a conspecific's gender (Whiting & Bateman 1999) or a male's fighting ability (Whiting *et al.* 2006). During close encounters, males use tongue-flicking to obtain chemical cues. Most male-male contests are settled using a visual signal, the UV reflective throat

(Whiting *et al.* 2006), which acts as an honest signal of status (Stapley & Whiting 2006). In the case of females, males use visual signals for initial gender recognition and thereafter approach the females using a stereotypical courtship display (Whiting & Bateman 1999). If females allow close enough approach, males will then tongue-flick the female's flanks and/or cloacal region (M. J. Whiting 1995, personal observation), presumably to assess reproductive status. The length of time young males (hereafter she-males) retain female-like coloration is probably a condition-dependent strategy because all males ultimately develop typical male (hereafter he-male) coloration. That is, because time to adult colour expression is variable, the switch point at which she-males become he-males could potentially be dependent on prevailing social conditions (e.g. presence and number of adult males). Males are brightly coloured, territorial and highly aggressive (Whiting 1999; Whiting *et al.* 2003, 2006). Females are drab brown and have dorsal stripes (Branch & Whiting 1997). As juveniles, males appear female-like and initial colour development occurs on the venter, where it is concealed. During this time, he-males may visually mistake she-males for females and may court them (M. J. Whiting, J. K. Webb & J. S. Keogh 2003, personal observation). However, once the colour begins spreading to the sides and dorsum, these males are chased and attacked by he-males (M. J. Whiting, J. K. Webb & J. S. Keogh 2003, personal observation). Examples of she-males, females and typical males are depicted in figure 1.

In this study, we investigated whether she-males can manipulate multiple signals to deceive a receiver. Specifically, we tested whether she-males conceal their identity from he-males using both visual and chemical (scent) signals. Finally, we examined the function and behavioural costs associated with dishonest signals. All of our experiments were performed in the wild.

## 2. MATERIAL AND METHODS

### (a) Study system

We conducted fieldwork during September 2003 at Augrabies Falls National Park (hereafter Augrabies; 28° 35' S, 20° 20' E), Northern Cape Province, South Africa. Flat lizards are rupicolous and, at Augrabies, favour the granitic banks of the Orange River. The Augrabies population is extremely dense, resulting in a high encounter rate and frequent interactions between individuals. Detailed descriptions of the study area can be found in Branch & Whiting (1997) and Whiting & Greeff (1997).

### (b) Chemical signal manipulation

We used hexane (Mason *et al.* 1989) to remove skin surface lipids from lizards. These individuals either served as scent donors or scentless controls or were labelled with extracted scent following scent removal (table 1). We randomly allocated females to one of three groups: *control female* (CF) in which scent was unmanipulated; *hexane control female* (HF) in which scent was removed; and *hexane female with she-male scent* (HFM) in which a female's scent was removed with hexane before being labelled with a she-male's scent. She-males were randomly allocated to the following groups: *control she-male* (CSM) in which scent was unmanipulated; *hexane she-male* (HSM) in which scent was removed; and *hexane she-male with female scent* (HSMF) in which a male's



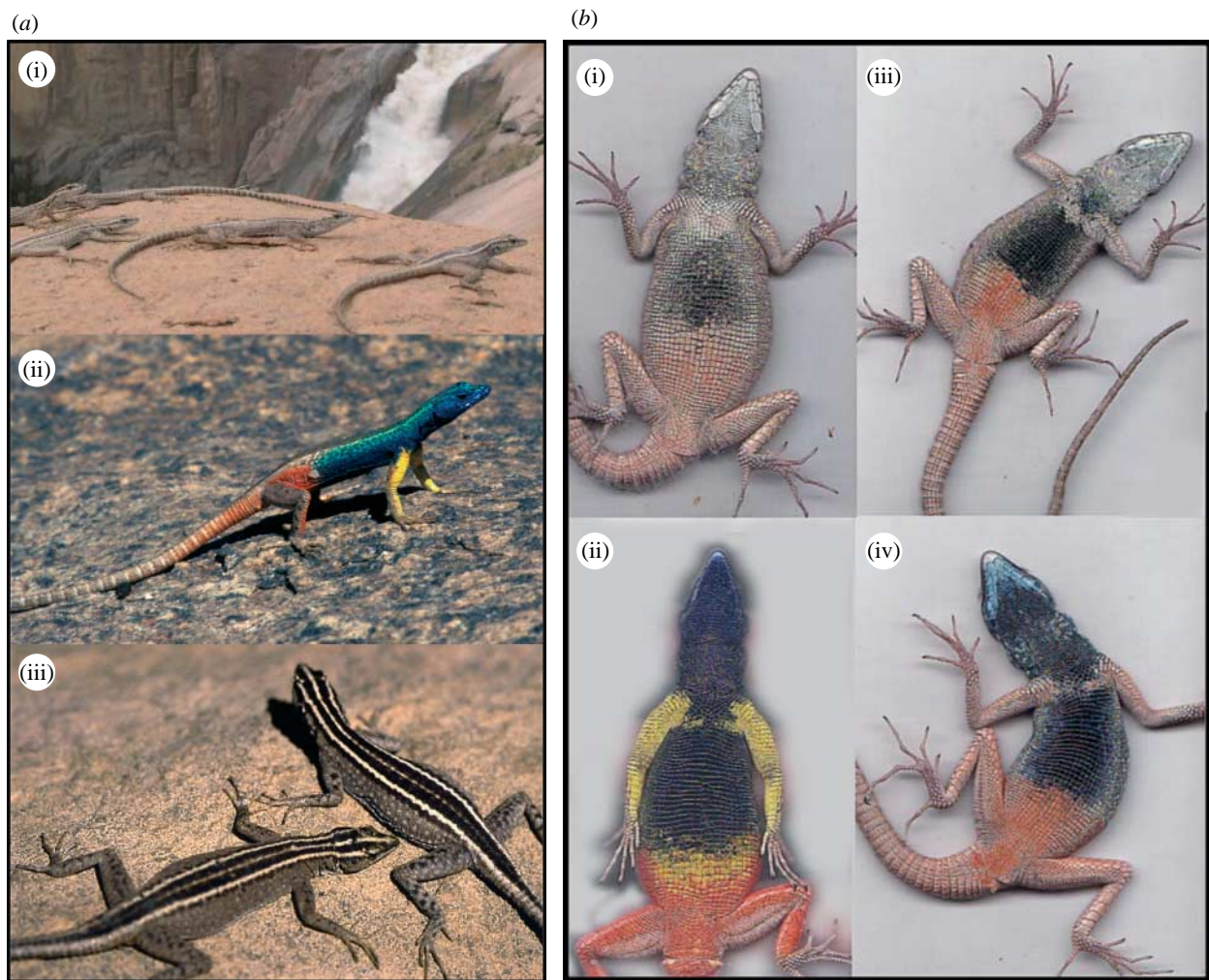


Figure 1. Examples of flat lizards (*P. broadleyi*). (a) Lizards in (i) could be either female or she-male, (ii) is a typical male and (iii) are typical females. (b) Ventral views are presented for (i) female, (ii) male and (iii)–(iv) she-male flat lizards.

Table 1. Breakdown of treatments and sample sizes used to test chemical discrimination by free-ranging *P. broadleyi* males. (All individuals used in the treatments were female, or female-like in appearance (she-males). Individuals were allocated either to an unmanipulated control group, a control group in which hexane was used to remove all scent, or a treatment group in which scent was removed using hexane and lizards were relabelled male or female. All test lizards were used only once, and free-ranging he-males ( $N=208$ ) were only presented with a single test lizard.)

treatment	description	<i>N</i>	gender	male scent	female scent	no scent
CF	control female	35	F		X	
CSM	control she-male	34	M	X		
HF	hexane female	35	F			X
HSM	hexane she-male	34	M			X
HFM	hexane female with male scent	34	F	X		
HSMF	hexane she-male with female scent	36	M		X	

scent was removed with hexane before being labelled with a female's scent. We did not include he-males as a treatment group because the response is predictable: residents immediately challenge rivals and chase them (Whiting 1999; Whiting *et al.* 2003, 2006). Furthermore, there would be no chemical sampling in this scenario (M. J. Whiting 1995, personal observation) and, as such, the trials would not be informative. Lizards (table 1) were then presented once to a free-ranging male using tethering. We tethered the treatment male to a 3 m pole using an approximate 1 m length of dental floss, tied loosely around its waist. For consistency, the same individuals always either prepared lizard treatments or conducted the tethering trials, but not both. All trials were blind such that

the presenter never knew which treatment he was presenting. To maintain independence we tested free-ranging males only once, over a broad area, and never worked in the same area twice. Free-ranging males showed the following reactions to the test animals: (i) continued courtship, (ii) aggression, or (iii) forced copulation attempts. We immediately terminated a trial if males were aggressive or attempted copulation.

#### (c) Visual signals and behavioural responses to chemical signals

We lowered the test animal several metres from the focal animal, in a visible location. For each trial, we recorded the following information: whether the focal animal approached

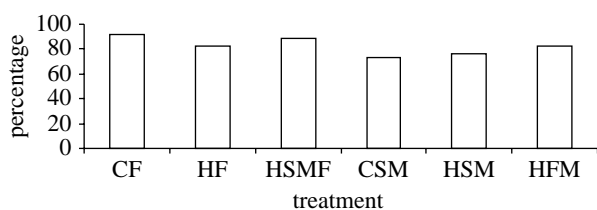


Figure 2. The percentage of individuals courted by free-ranging males based on visual signals alone (prior to chemical sampling). Total sample sizes including both courted and non-courtied individuals are given in table 1.

using courtship; time to and time of first tongue-flick (TF); total number of tongue-flicks; whether the focal animal continued courtship following tongue-flicking; interaction time since first tongue-flick; total interaction time; and whether the focal animal attempted copulation and/or any aggressive behaviours. Duration of behaviours was recorded using stopwatches.

#### (d) Statistical analyses

Prior to conducting parametric procedures, we checked for normality using Kolmogorov–Smirnov tests and tested for homoscedacity using Bartlett’s tests. Where necessary, we log-transformed data to meet the assumptions of parametric statistics. To assess scent recognition by males, we scored whether courting males continued with courtship after tongue-flicking the test animal. We used logistic regression in which an outcome is binary (court or not) to calculate the probability of a male courting a test animal in relation to a reference group (CFs). These odds ratios are calculated by taking the exponential of the coefficients of the model. Finally, we used logistic regression to test for significant differences in the probability of continued courtship among treatments.

### 3. RESULTS

#### (a) Visual signals

Free-ranging males readily courted test lizards from all treatment groups (figure 2; logistic regression: Wald  $\chi^2_5=5.5$ ,  $p=0.36$ ), suggesting that she-males are able to deceive males using visual signals. Furthermore, the odds of a male courting an individual from any of the treatment groups were similar to the odds of courting a CF (table 2; logistic regression:  $p>0.05$  in each case). In particular, test males were 0.46 times as likely to court a CF compared with a CSM based on visual signals alone (Wald  $\chi^2_1=0.38$ ,  $p=0.54$ ).

#### (b) Chemical signals

Scent treatment group had a significant effect on whether males continued courting test lizards after chemical sampling (logistic regression: Wald  $\chi^2_5=16.82$ ,  $p=0.005$ ). Males based courtship on the presence of female scent irrespective of the true gender of the test lizard such that treatments with female scent had the highest frequency of courtship and treatments with male scent or no scent the lowest frequency of courtship (figure 3; table 3).

Following chemical sampling (first tongue-flick), interaction time among treatments was not significantly different (ANOVA,  $F_{5,201}=1.86$ ,  $p=0.1$ ; see fig. S1 in the electronic supplementary material). However, if we group

Table 2. (a) Maximum-likelihood estimates testing for significant differences among treatment groups in the probability of courtship based purely on visual signals (prior to chemical sampling), in relation to the reference group (CFs). (The probability of a he-male courting a test lizard was independent of treatment.) (b) Odds ratio estimates of a he-male courting a lizard belonging to a treatment group compared with CFs based only on visual signals.

parameter	d.f.	estimate	s.e.	Wald $\chi^2$	$p$ -value
<i>(a)</i>					
intercept	1	3.219	1.020	9.963	0.002
CSM	1	−0.777	1.258	0.381	0.537
HF	1	−1.661	1.159	2.054	0.152
HFM	1	−1.347	1.153	1.366	0.243
HSM	1	−2.079	1.098	3.588	0.058
HSMF	1	−1.273	1.151	1.222	0.269
<i>(b)</i>					
effect		point estimate		95% Wald confidence limit	
CSM vs CF		0.460		0.039–5.419	
HF vs CF		0.190		0.020–1.841	
HFM vs CF		0.260		0.027–2.489	
HSM vs CF		0.125		0.015–1.075	
HSMF vs CF		0.280		0.029–2.674	

treatments according to whether they had male or female scent and include controls according to their true gender (CF, HF, HSMF versus CSM, HSM, HFM), free-ranging males spent significantly ( $t_{205}=205$ ,  $p=0.012$ ) more time interacting with the ‘female’ group.

Following a log transformation, the number of tongue-flicks directed at test animals was homoscedastic (Bartlett’s  $\chi^2_5=4.3$ ,  $p=0.51$ ), and all treatments were normally distributed (Kolmogorov–Smirnov test,  $D>0.1$ ,  $p>0.13$ ). The mean number of tongue-flicks by each treatment group were not significantly different (ANOVA,  $F_{5,201}=1.36$ ,  $p=0.24$ ; see fig. S2 in the electronic supplementary material).

#### (c) The consequences of deception

The frequency of forced copulation attempts was significantly higher in the group containing females or she-males with female scent (CF, HF and HSMF) compared with the group containing she-males, or females with male scent (CSM, HSM and HFM; figure 4;  $\chi^2_1=12.46$ ,  $p=0.0001$ ).

### 4. DISCUSSION

Male *Augrabies* flat lizards can delay the onset of colour expression and thereby mimic females, even though they are sexually mature. This resemblance was sufficient to conceal their true gender, such that similar numbers of he-males courted all treatment groups, regardless of their gender, on the basis of visual signals alone. However, based on the responses of he-males to test lizards, our experiment demonstrated that she-males do not mimic female pheromones. Females labelled with male scent and CSMs were very rarely courted following tongue-flicking and were sometimes met with an aggressive response (18% of trials compared with 0% for CFs). Conversely,



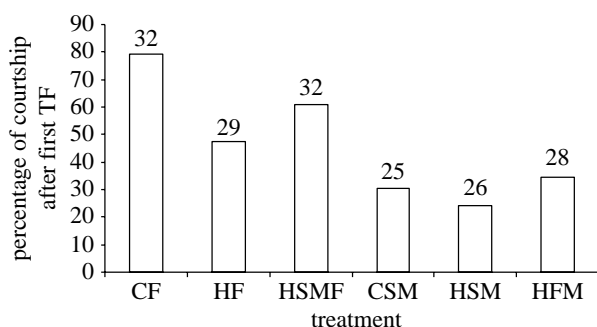


Figure 3. The percentage of test individuals that were courted by free-ranging males following chemical sampling via tongue-flicking. Only individuals that approached the test animal using courtship are included here. Sample sizes are indicated above the bars.

Table 3. (a) Maximum-likelihood estimates testing for significant differences among treatment groups in the probability of continued courtship after tongue-flicking, in relation to the reference group (CFs). (He-males were significantly more likely to court CFs than any treatment with male scent (CSM and HFM) and any treatment that lacked scent (HF and HSM); but he-males were not more likely to court she-males labelled with male scent (HSMF) compared with CFs.) (b) Odds ratio estimates of a he-male courting a lizard belonging to a treatment group compared with CFs based on chemical signals.

parameter	d.f.	estimate	s.e.	Wald $\chi^2$	<i>p</i> -value
(a)					
intercept	1	1.335	0.503	7.055	0.008
CSM	1	-2.162	0.677	10.203	0.001
HF	1	-1.440	0.681	4.474	0.034
HFM	1	-1.971	0.650	9.193	0.002
HSM	1	-2.082	0.645	10.413	0.001
HSMF	1	-0.900	0.634	2.012	0.156
				95% Wald confidence limit	
(b)					
effect	point estimate				
CSM vs CF	0.115		0.031–0.434		
HF vs CF	0.237		0.062–0.900		
HFM vs CF	0.139		0.039–0.498		
HSM vs CF	0.125		0.035–0.442		
HSMF vs CF	0.407		0.117–1.410		

CFs and HSMFs were courted by he-males following tongue-flicking and forced copulation attempts were highest in these groups (and the HF group). Also, when approached by he-males, she-males initially moved away and avoided male tongue-flicks. This is consistent with our observations of free-ranging she-males: close contact with he-males appears to be avoided at all costs. Therefore, while she-males exploit visual signals as a dishonest signal, their scent is a honest signal of their gender.

Multiple signals are used by most animals because they either reinforce information ('backup messages') or convey slightly different information ('multiple messages'), usually about the signaller's condition, to a receiver (Johnstone 1996). Furthermore, different sensory modalities (e.g. acoustic, visual, chemical) are effective under specific environmental conditions (Johnstone 1997;

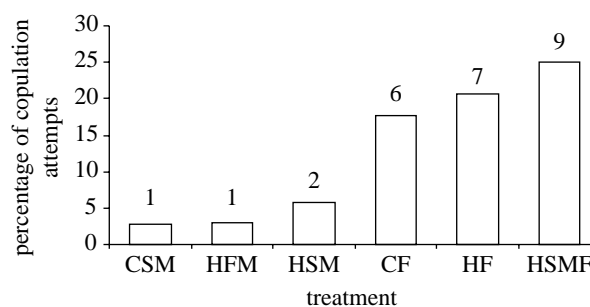


Figure 4. The percentage of test animals that experienced copulation attempts by free-ranging males. See text for statistical analysis. Sample sizes are indicated above the bars.

Maynard Smith & Harper 2003; Hibbitts *et al.* 2007). Therefore, for animals to convey effective signals, multiple signal types might be employed depending on the environmental conditions at the time of signalling. Traditionally, most studies of multiple signalling have focused on mate choice (reviewed in Peschke 1987; Candolin 2003) or contest competition (Stuart-Fox *et al.* 2006; Whiting *et al.* 2006). In the context of female mimicry, the focus has been on single traits (but see Shine & Mason 2001); therefore, we have a very poor understanding of how receivers deal with multiple signals. While deception of visual signals such as pattern, colour and behaviour are relatively common (Brower 1988), mimicry of pheromonal signals, although best known for insects (Peschke 1987; Forsyth & Alcock 1990; Dettner & Liepert 1994; Cardé & Bel 1995), is extremely rare among vertebrates. In vertebrates, the only documented case of pheromonal mimicry in the context of female mimicry is the garter snake *T. s. parietalis* (Mason & Crews 1985). Interestingly, this is no longer considered an alternative reproductive tactic because female mimicry is a transitory phase adopted by probably all males in the first few days following emergence from hibernation (Shine *et al.* 2000). Among invertebrates, males of two species of rove beetle mimic female pheromones to avoid aggression from larger males (Peschke 1987; Forsyth & Alcock 1990). The nature of chemical mimicry precludes it from being a common phenomenon (Alberts 1992). Typically, a chemical signal is composed of numerous different components of variable molecular weight, aromaticity and volatility. Furthermore, chemical mimicry is far less likely when the biochemistry of odour production is tightly linked to nutritional status (Alberts 1992). In sexually selected species in which males are colourful, expression of colour is a natural ontogenetic process. Therefore, halting or reversing the expression of a normal physiological process may be a simpler process and therefore a lot more common. For example, depending on the prevailing social conditions, males of the cichlid *Astatotilapia burtoni* are able to rapidly switch between a non-territorial morph that mimics females and a colourful territorial morph (Korzan *et al.* 2008).

While she-male flat lizards are only able to deceive rival he-males with visual and not chemical signals, this may still be adaptive simply because the deception can be maintained through behavioural means. When in close quarters, she-males can avoid being chemically sampled by a short rapid movement to just beyond the reach of a male's tongue-flick. Many females move short distances away from courting males, so this behaviour is not unlike a

female shunning the advances of a courting male. Finally, for she-males to successfully copulate with females, they may still require male scent as a necessary precursor during female mate choice. If this is true, then the fitness consequences of retaining male scent may override any benefits of mimicking female scent, particularly if the she-males are able to prevent males from chemically sampling them in the first place.

What are the benefits of female mimicry to she-males? Young males that are just developing adult male coloration on readily visible areas of the body (head and flanks) are frequently chased or attacked by older males that have more fighting experience and are typically larger. In Augrabies flat lizards, the best fighters have throats that are rich in UV while poor fighters have more violet throats (Whiting *et al.* 2006). She-males have little UV and almost never engage in contest competition (M. J. Whiting, J. K. Webb & J. S. Keogh 2003, unpublished data). By suppressing colour expression, males are able to mimic females and avoid the obvious risks associated with fighting that include injury, energetic costs and, possibly, predation. All males ultimately develop typical adult male coloration. Therefore, being a she-male is a transitory phase. The durations of these transitory phases are frequently condition-dependent strategies, which also occur in such diverse taxa as beetles (Peschke 1987; Forsyth & Alcock 1990), cuttlefish (Hanlon *et al.* 2005), cichlid fish (Korzan *et al.* 2008), garter snakes (Shine *et al.* 2000) and lizards (Martin & Forsman 1999). Although she-male flat lizards mimic females using visual and not chemical signals, by staying one step ahead of males and avoiding chemical contact, they are able to successfully maintain this deception. Consequently, she-males are able to approach, tongue-flick and court females in the presence of a resident male (M. J. Whiting, J. K. Webb & J. S. Keogh 2003, personal observation). Therefore, female mimicry in flat lizards is probably adaptive and favoured by sexual selection through its role as an alternative reproductive tactic.

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