

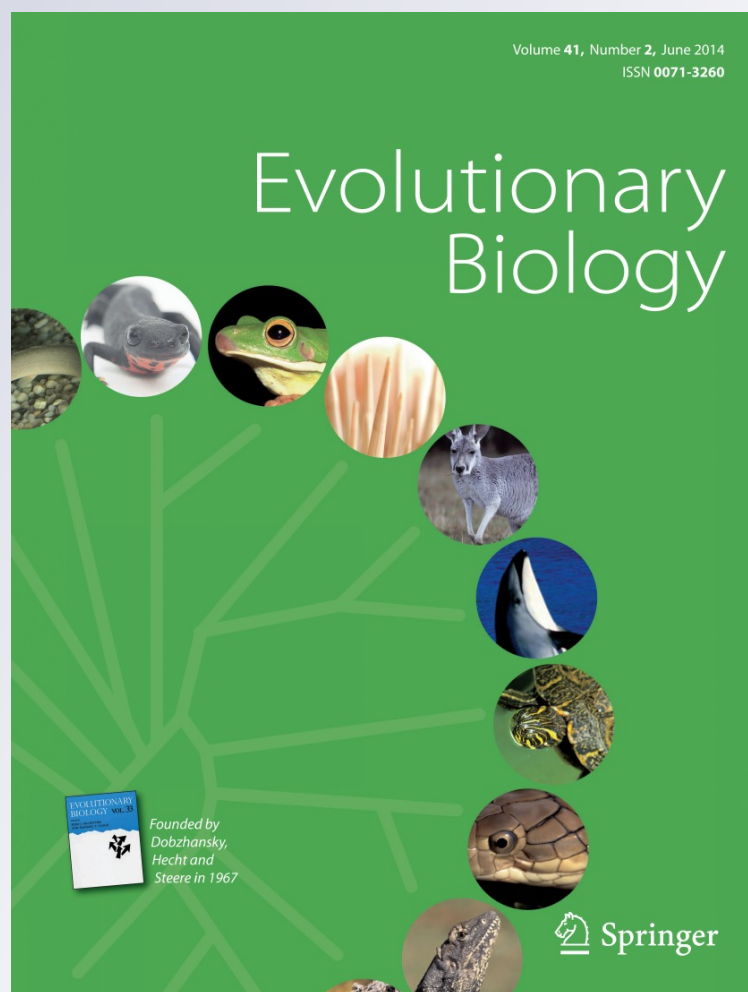
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# Sexual Selection and Dynamics of Jaw Muscle in *Tupinambis* Lizards

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**Abstract** Sexual dimorphism patterns provide an opportunity to increase our understanding of trait evolution. Because selective forces may vary throughout the reproductive period, measuring dimorphism seasonally may be an interesting approach. An increased male head size may be important in intersexual and intrasexual interactions. In *Tupinambis* lizards, a big head is attributed in part to a large adductor muscle mass. Competition for mating can differ in species with different sex ratio and different degrees of sexual size dimorphism. We examined sexual differences in mass of the pterygoideus muscle, its temporal variation throughout the reproductive period and the relationship between muscle and reproductive condition in *Tupinambis merianae* and *T. rufescens*. We characterized sexual size dimorphism and sex ratio in both species. Mature males had larger jaw muscles than mature females in both species, mainly during the reproductive season. The dimorphism in jaw muscle was due to an increase in muscle mass in sexually active males. Seasonal increases in muscle mass and variation between immature and mature individuals suggest that the jaw muscle might be a secondary sexual character. We propose that the pterygoideus muscle may act as a signal of reproductive condition of males because it is associated with testis size and sperm presence. The patterns of sexual dimorphism in jaw muscle in both species were similar; however, the comparison shows how sexual characters remain dimorphic in different

competition contexts and in species with different degrees of body size dimorphism. Our results suggest that jaw muscle as sexual character could be influenced by inter- and intrasexual selective pressures.

**Keywords** Secondary sexual character · Sexual dimorphism · Seasonal variation · Pterygoideus muscle · *Tupinambis merianae* · *Tupinambis rufescens*

## Introduction

Differentiation between males and females in morphology, performance, behaviour and many other traits has long been a paradigm for evolutionary biologists (Darwin 1871; Andersson 1994). Patterns of sexual dimorphism provide an opportunity to increase our understanding of trait evolution because they result from selection forces that act differentially on individuals of each sex (Cox et al. 2003; Corl et al. 2009). Sexual size dimorphism is common in reptiles (Schoener 1977; Stamps 1983) and has been documented in lizards, with males typically being larger than females (Fitch 1981; Cox et al. 2007). Another important aspect to consider is sexual dimorphism of different body parts (Anderson and Vitt 1990; Herrel et al. 1996; Butler et al. 2000); indeed, the relative size of different body parts can be very informative of the selective pressures imposed on each sex (Cooper and Vitt 1989; Braña 1996; Hews 1996; Butler and Losos 2002; Kratochvil et al. 2003). Several hypotheses have been proposed to explain the evolution of morphological differences between sexes, including differential niche utilization, intersexual food competition, and sexual selection (Hendrick and Temeles 1989; Andersson 1994). In a reproductive context, sexual

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dimorphism of structures may be the result of intrasexual selection pressures when individuals compete for mates (Stamps 1983; Cox et al. 2003) and of intersexual selection pressures when signals for mate preference are identified (Cooper and Vitt 1993; Irschick et al. 2007). The traditional focus on the design of static signals such as ornaments has failed to fully explain sexual selection in a number of important systems (Mowles and Ord 2012). In addition, unravelling mechanisms underlying the evolution of sexual dimorphism can be complicated due to variation in the selective pressures acting during different periods of activity. In some species, such as *Anolis carolinensis*, the dewlap area changes seasonally, being larger in the spring reproductive season (Irschick et al. 2006). Because the strength of selective forces may vary at different moments during the reproductive period, measuring dimorphism over time and interpreting it as a dynamic trait may be an interesting approach to the understanding the evolution of sexual traits.

Secondary sexual traits evolve through the process of sexual selection, either via female choice, male–male competition or a combination of both (Berglund et al. 1996). An increased male head size may simultaneously be important in intersexual interactions (Herrel et al. 1996, 1999; Gvozdik and Van Damme 2003) and intrasexual interactions (Vitt and Cooper 1985; Bull and Pamula 1996; Gvozdik and Van Damme 2003). During copulation the male lizard typically bites the female on the back of the neck as he mounts her (Pough et al. 2001). Another important role of biting lies in determining the outcome of aggressive interactions (Lailvaux et al. 2004; Huyghe et al. 2005; Lappin and Husak 2005; Husak et al. 2006). Bite force is strongly correlated with body and head sizes in several lizard taxa (Anderson et al. 2008; Herrel et al. 2009) among which *Tupinambis* males exhibit larger body size than females (Anderson and Vitt 1990; Fitzgerald et al. 1991). A big head in *Tupinambis* lizards is attributed in part to a large adductor muscle mass (Rieppel 1980), with the pterygoideus muscle forming a large mass around the posterior portion of the lower jaw (McBrayer and White 2002). Individuals with greater heads could be more successful in male–male contest where jaws are considered as armaments (Bull and Pamula 1996). The expression of sexual characters often shows evidence of condition dependence. For example, some secondary sexual traits develop at sexual maturity, which generally enhances trait expression (Moller 1996). Traits that increase considerably in relative size with maturation are likely to be those that are necessary for successful breeding (Hendry and Berg 1999). Moreover, secondary sexual characters can indicate the reproductive condition or reproductive potential (Lailvaux and Irschick 2006). By choosing males with sexual ornaments, females would also benefit if such selection maximized the chances of females to mate with

high quality fertile males (Sheldon 1994). Another function of male sexual character could be that of signalling to other males the competitiveness of the ejaculate (Malo et al. 2005). Thus, sexual selection can operate through different processes in the same structure.

Competition for mating opportunities among males has long been recognized as a potent selective pressure shaping the evolution of secondary sexual traits (Simmons and Emlen 2006). Competition may differ in species with different sex ratio of individuals qualified to mate (Ahnesjö et al. 2001; de Jong et al. 2009) and has important consequences for sexual selection (Kvarnemo and Ahnesjö 1996). Variation in body size, sexual characters and gonadal investment among male lizards may be related to differences in reproductive strategies (Dial et al. 2008). Body size may be advantageous for reproductive behavior (Olsson 1993). Furthermore, interspecific variation in the degree of sexual body size dimorphism may provide additional information to interpret variation in sexual traits. Interpreting the relationship among sexual body size dimorphism, sex ratio, and jaw muscle traits between related species may contribute to our understanding of selective pressures acting on sexual characters.

Interpreting the proximate causes that lead to morphological differentiation between and within males and females can be crucial to elucidating the evolutionary pressures acting on each sex and species (Kaliontzopoulou et al. 2008). Accordingly, *Tupinambis merianae* and *T. rufescens* provide a good model system for studying evolution of sexual traits and seasonal changes therein because they are closely related species (Cabaña et al. 2013) and share bioecological traits (Cardozo et al. 2012). Their reproductive behaviour is limited to a period of the active season (Fitzgerald et al. 1991, 1993), and larger *Tupinambis* individuals are more aggressive and dominant than smaller ones (Herrel et al. 2009).

In the present study, we characterized the pterygoideus muscle in *T. merianae* and *T. rufescens* in a sexual selection context. First, we examined sexual differences in the jaw muscle in mature and immature individuals. Second, we examined the intrasexual variation, temporal dynamics of jaw muscle and the relationship between jaw muscle and reproductive condition. Finally, we characterized sexual size dimorphism and sex ratio in both species to interpret variations in jaw muscle size.

## Methods

### Species and Study Area

*Tupinambis merianae* and *T. rufescens* are big-sized Teiidae lizards that reach large body sizes at adulthood (Avila-Pires 1995; Andrade and Abe 1999) and that undergo a

great shift in body size during ontogeny. They are geographically close species that occur in the southernmost area of the distribution of the genus in South America (Cei 1993; Colli et al. 1998). These species overwinter in burrows and emerge during the warm season (October to March); they are seasonal breeders that reproduce from about October to January (Fitzgerald et al. 1991, 1993). Both species are included in Appendix II of the Convention on International Trade of Endangered Species of Wild Fauna and Flora (CITES); in Argentina, commercial harvest is allowed (Porini 2006; Res. 11/2011, Secretaría de Ambiente y Desarrollo Sustentable de la Nación). Scientific studies based on the examination of specimens collected for the international skin trade provided important knowledge of the biology of the species (Shine et al. 1999).

#### Data Collection

*Tupinambis* individuals were caught weekly from wild populations by local authorized hunters in central Argentina (*T. rufescens*: 29°35'W, 64°10'S to 31°10'W, 63°15'S and *T. merianae*: 30°55'W, 63°40'S to 31°45'W, 62°15'S) between October and March. We are authorized by the government environmental agencies for scientific capture, and we selected and accompanied authorized local people to standardize the sampling protocol with the aim of avoiding sex and size bias in capture rates. Specimens were killed for the legal skin trade, in accordance with AVMA Guidelines on Euthanasia (AVMA 2007). We recorded species, date, sex and sexual maturity (mature or immature). We measured the snout vent length (SVL) to the nearest 0.5 cm with a ruler and body mass (BM) to the nearest 50 g with a balance. In males we dissected and weighed the mass of both testes (TM) to the nearest 0.1 g using an electronic balance (Traveler TA302; OHAUS; New Jersey, USA). We determined sex and sexual maturity of lizards by inspecting the reproductive organs. Females were considered reproductive if they had oviductal eggs or enlarged vitellogenic follicles. In males, we recorded the presence or absence of sperm in epididymides; samples of seminal fluid were examined under a phase contrast microscopy (model eclipse Ti; Nikon Instruments Inc.; Tokyo, Japan). We categorized mature males as sexually active males (with presence of sperm) or males without sperm. The SVL of the smallest reproductive female and male was used to estimate minimum size at sexual maturity (Madsen et al. 2006; Cardozo and Chiaraviglio 2011). In total, we evaluated 693 *T. merianae* and 130 *T. rufescens* individuals.

#### Muscle Dissection

We dissected the pterygoideus muscle for all individuals. We selected the superficial pterygoideus layer because it is

active during the power phase of biting in *Tupinambis* lizards and has an important role in both force production and jaw stabilization (Rieppel 1980; McBrayer and White 2002). The superficial pterygoideus muscle mass (PMM) was determined to the nearest 0.1 g using an electronic balance (Traveler TA302; OHAUS; New Jersey, USA). To show values for relative muscle mass in the figures, we used an index of PMM, which was calculated as PMM (g) divided by BM (g), multiplied by 100.

#### Data Analyses

An analysis of covariance (ANCOVA) was used to assess morphological changes, independent of variation in body size. Muscle mass, BM and TM were log<sub>10</sub> transformed. We compared PMM between sexes with an ANCOVA using BM as covariate in each species. We also compared between species with an ANCOVA using BM as covariate. We compared temporal changes in muscle mass using an ANCOVA, with sampling month as class effect and BM as covariate. We assessed the difference in PMM among mature males sampled during the breeding season using an ANCOVA, with presence or absence of sperm as class effect and body mass as covariate. We tested for homogeneity of slopes among treatment groups with a treatment by covariate interaction term, which we retained in model when significant and omitted when non significant. To compare the relative amount of variation in PMM between sexes we used the coefficient of variation (CV). We used Levene's test to examine whether the variance of PMM differed among months. Pterygoideus muscle mass was regressed on BM. The slope of these regressions estimated the relative relationships: a slope of 1 indicated isometry, a slope greater than 1.0 indicated positive allometry, and a slope less than 1.0 indicated negative allometry (Bonduriansky 2007; Araujo and Tschinkel 2010). We calculated sex ratio using sexually mature lizards during the breeding season; to test for difference in the proportion of sexes we used a Chi square test. We used SVL to calculate an index of sexual size dimorphism (SSD) (Lovich and Gibbons, 1992). A negative SSD value indicated that males were the larger sex and a positive SSD value indicated the opposite. All statistical analyses were made using SPSS 16.0 (SPSS 16.0 Inc., Chicago, IL, USA).

#### Results

The smallest sexually active male was 29.5 cm SVL for *T. merianae* and 30.5 cm SVL for *T. rufescens*. The smallest sexually active female was 32 cm SVL in both species. Pterygoideus muscle mass was greater in mature males than in mature females in each species (Table 1). In



immature individuals, PMM was similar between sexes in each species (Table 1), whereas it differed between species in mature males (ANCOVA: species effect term  $F_{1, 449} = 5.95, P = 0.015$ ), being higher in *T. rufescens*; by contrast, PMM did not differ between species in mature females (ANCOVA: species effect term,  $F_{1, 292} = 0.12, P = 0.732$ ).

We observed a positive relationship between PMM and BM in mature males and females of both species (Fig. 1) (*T. merianae* males:  $F_{1,363} = 1,799.12, r = 0.83, P < 0.001$ ; *T. merianae* females:  $F_{1,274} = 676.03, r = 0.71, P < 0.001$ ; *T. rufescens* males:  $F_{1,85} = 409.13, r = 0.83, P < 0.001$ ; *T. rufescens* females:  $F_{1,17} = 15.73, r = 0.45, P < 0.001$ ), but with a different slope between sexes (Table 1). Slopes were steeper for males than for females. The slope for each sex was similar between species (ANCOVA: Males: interaction term species\*covariate log10BM  $F_{1,448} = 0.69, P = 0.407$ ; Females: interaction term species\*covariate log10BM  $F_{1,291} = 0.69, P = 0.406$ ).

We observed differences in the CV of PMM between sexes in both species, which was approximately twice as high in males as in females for both species (CV *T. merianae* mature males: 73.68; CV *T. merianae* mature females: 34.19; CV *T. rufescens* mature males: 65.06; CV *T. rufescens* mature females: 26.66). The variance of PMM varied among months in *T. merianae* males; in *T. rufescens* males, although there were no statistical differences, a trend to temporal variation in CV is observed in Fig. 2 (Levene's test: *T. merianae*:  $F_{5,359} = 3.57, P = 0.004$ ; *T. rufescens*:  $F_{5,81} = 2.21, P = 0.061$ ). In females, the variance was homogeneous among months (Levene's test: *T. merianae*:  $F_{5,270} = 0.394, P = 0.853$ ; *T. rufescens*:  $F_{4,14} = 2.625, P = 0.080$ ). Pterygoideus muscle mass varied among months in mature males (ANCOVA: *T. merianae*: month effect term,  $F_{5,353} = 4.28; P < 0.001$ ; *T. rufescens*: month effect term,  $F_{5,80} = 2.75; P = 0.024$ )

(Fig. 2). The greatest PMM was observed in *T. merianae* males in the samples taken in November and December and in *T. rufescens* males in November.

During the period of sperm presence (October–December), males with sperm in epididymides showed greater PMM and TM than mature males without sperm (Table 2). The analysis of males with sperm showed that PMM and TM were similar between species (ANCOVA: PMM:  $F_{1,148} = 3.35; P = 0.069$ ; TM:  $F_{1,146} = 3.582; P = 0.06$ ). The difference in PMM between sexually active males and mature females during reproductive period (October–December) was similar between species (ANCOVA PMM 2 factors species and sex: interaction term species\*sex  $F_{5,387} = 0.05, P = 0.827$ ).

Pterygoideus muscle mass was significantly associated with TM in sexually active males in both species during the breeding season. In addition, PMM was positively correlated with TM (Table 3) and the slope was similar between species (ANCOVA: interaction term  $F_{1,146} = 1.82, P = 0.176$ ).

*Tupinambis rufescens* presented greater sexual size dimorphism than *T. merianae*. The index of SSD for *T. merianae* was -0.04 (ANOVA SVL,  $F_{1,661} = 31.93; P < 0.001$ ) and -0.15 for *T. rufescens* (ANOVA SVL,  $F_{1,115} = 39.79; P < 0.001$ ). During the breeding season (October–December), mature sex ratio of *T. rufescens* was = 4.11: 1 (70 males and 17 females) (Chi Square Test:  $\chi^2 = 32.29; df = 1; P = 0.001$ ) and mature sex ratio of *T. merianae* was = 1.41: 1 (325 males and 245 females) (Chi Square Test:  $\chi^2 = 11.23; df = 1; P = 0.001$ ).

**Discussion**

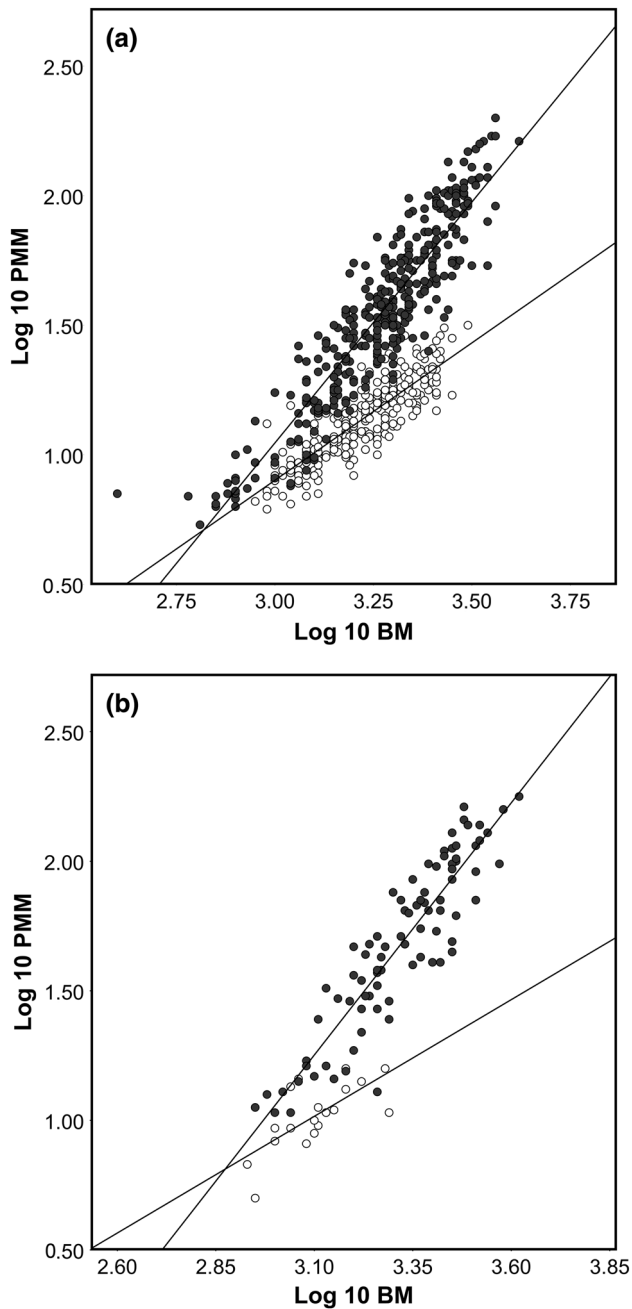
*Tupinambis* males and females might be subjected to different selective pressure intensity on jaw muscles because

**Table 1** Mean of pterygoideus muscle mass (PMM) and ANCOVA results for log10-transformed PMM with sex as class effect and log10-transformed body mass (BM) as covariate for immature and mature individuals of both species studied

Species	Maturity class	Sex	N	Mean PMM (g) ± SE	Sex (F)	Covariate Log10 BM (F)	Interaction sex × Cov (F)	Model R <sup>2</sup>
<i>Tupinambis merianae</i>	Immature (df = 1,18)	Males	9	6.07 ± 1.52	0.11	53.67***	–	0.722
		Females	12	5.16 ± 0.45				
<i>Tupinambis merianae</i>	Mature (df = 1,637)	Males	365	46.09 ± 1.77	100.68***	1,772.44***	132.73***	0.886
		Females	276	14.43 ± 0.30				
<i>Tupinambis rufescens</i>	Immature (df = 1,8)	Males	4	5.16 ± 1.10	2.51	46.19***	–	0.841
		Females	7	6.26 ± 0.56				
<i>Tupinambis rufescens</i>	Mature (df = 1,102)	Males	87	62.43 ± 4.26	9.04**	79.12***	10.68**	0.891
		Females	19	10.88 ± 0.65				

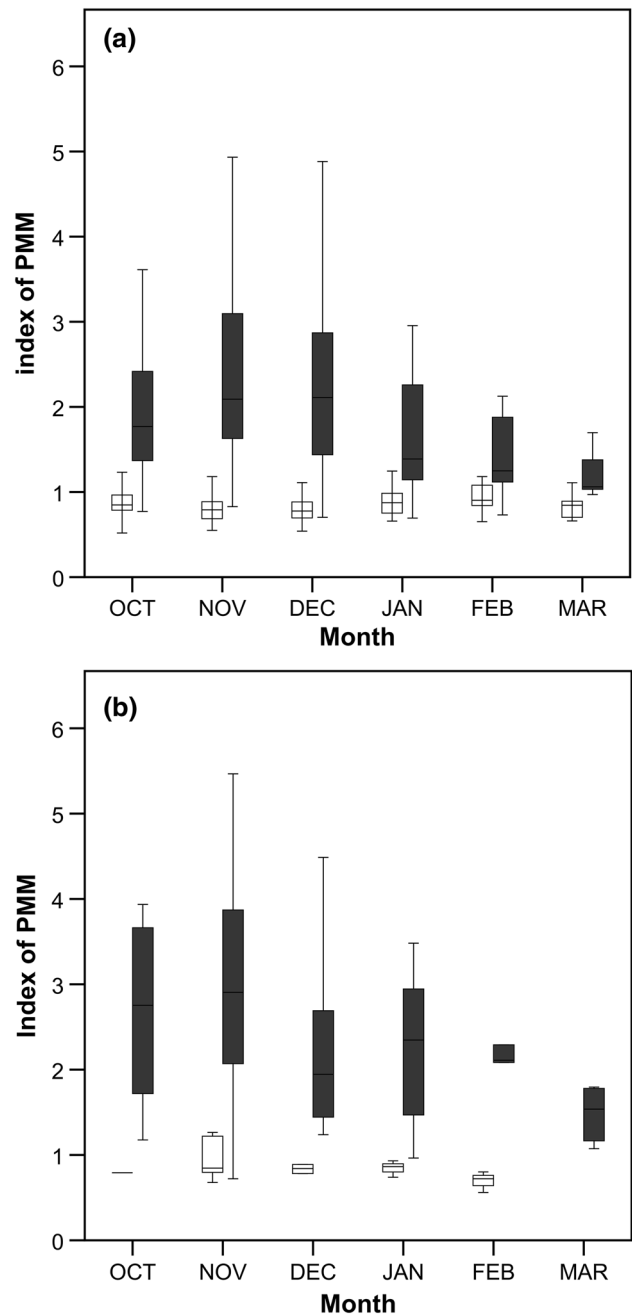
Pterygoideus muscle mass is expressed in grams (g)

\*\*\*  $P < 0.001$ ; \*\*  $P < 0.01$ ; \*  $P < 0.05$



**Fig. 1** Relationship between pterygoideus muscle mass (PMM) and body mass (BM) for mature males (*solid symbols*) and mature females (*empty symbols*) of *T. merianae* (a) and *T. rufescens* (b). Least-square regression lines are shown for males and females of each species (*T. merianae* males:  $y = -4.53 + 1.86 x$ ; *T. merianae* females:  $y = -2.27 + 1.06 x$ ; *T. rufescens* males:  $y = -4.78 + 1.95 x$ ; *T. rufescens* females:  $y = -1.75 + 0.89 x$ )

the pterygoideus muscle mass was sexually monomorphic in immature individuals and dimorphic at maturity. Moreover, males of both lizard species had larger jaw muscles than females. The sexual dimorphism observed in the jaw muscle was due to an increase in muscle mass in sexually active males. The results obtained in *T. merianae*



**Fig. 2** Plots of mean PMM index of mature males (*grey*) and females (*white*) of *T. merianae* (a) and *T. rufescens* (b). Presence of sperm: October–December

and *T. rufescens* indicate important sexual variation in terms of temporal dynamics of the pterygoideus muscle. Seasonal increase of muscle mass during the reproductive period and variation between immature and mature individuals can provide important insights into the function of jaw muscle as a secondary sexual character. Our data on wild populations of *T. merianae* and *T. rufescens* reveal similar patterns of sexual dimorphism in jaw muscle and temporal variation.

**Table 2** Means of pterygoideus muscle mass (PMM) and testis mass (TM) of mature males with and without sperm in epididymides during the breeding season (presence of sperm: October–December) and

ANCOVA results for log transformed data with presence of sperm as class effect and log10-transformed body mass (BM) as covariate

		With sperm (g) ± S.E	Without sperm (g) ± S.E	Sperm class ( <i>F</i> )	Covariate Log Body mass ( <i>F</i> )
<i>Tupinambis merianae</i>	PMM (df = 1,194)	55.07 ± 3.70 ( <i>N</i> = 103)	35.64 ± 2.67 ( <i>N</i> = 94)	76.77 ***	1,157.53 ***
	TM (df = 1,195)	5.93 ± 0.29 ( <i>N</i> = 102)	4.11 ± 0.30 ( <i>N</i> = 96)	23.76 ***	83.22 ***
<i>Tupinambis rufescens</i>	PMM (df = 1,56)	77.30 ± 6.35 ( <i>N</i> = 45)	37.61 ± 8.53 ( <i>N</i> = 14)	17.85 ***	351.56 ***
	TM (df = 1,54)	8.27 ± 0.67 ( <i>N</i> = 44)	4.52 ± 0.56 ( <i>N</i> = 13)	4.01 *	23.30 ***

Pterygoideus muscle mass and testis mass are expressed in grams (g)

\*\*\* *P* < 0.001; \*\* *P* < 0.01; \* *P* < 0.05

**Table 3** Regression results for the relationship of log10- transformed testis mass (TM) with total log10-transformed pterygoideus muscle mass (PMM) in sexually active males of the two species studied

	<i>N</i>	<i>R</i> <sup>2</sup>	<i>P</i>	Slope	<i>a</i>
Log10 TM <i>Tupinambis merianae</i>	103	0.27	0.001	0.57	1.24
Log10 TM <i>Tupinambis rufescens</i>	45	0.46	0.001	0.79	1.12

*R*<sup>2</sup> squared correlation coefficient, *P* *P* value of *R*<sup>2</sup>, *Slope*, *a* intercept

It has been hypothesized that sexual selection would lead to the evolution of positive allometry, and that positive allometry would be a characteristic attribute of sexually selected traits (signal and weapon traits) (Petrie 1992; Kodric-Brown et al. 2006). Both in *T. merianae* and *T. rufescens*, the differences in the relationships between jaw muscle mass and body mass would be most likely related to sex. In females, this relationship was isometric, whereas in males jaw muscle increased more than proportional with increasing body size. Several studies have shown a direct link between relative head size and the ability to win male–male contests (Hews 1990; Molina Borja et al. 1998; Herrel et al. 2001; Gvozdik and Van Damme 2003). Moreover, during intersexual interactions (i.e., courtship, copulation), males may benefit from increased bite performance, because males with great muscle mass will be able to grasp a female to copulate (Gvozdik and Van Damme 2003), a behaviour observed in *Tupinambis merianae* (personal observation). When the male can grasp by biting the female, it will succeed to copulate with her. In addition, if males fight between them, males with high biting force might be favored. Pterygoideus muscle can have multiple functions and individuals with greater heads could be more successful in intrasexual contest and intersexual interaction where jaws are considered as armaments. Large body size can be considered a trait that is also involved in reducing the relative cost of carrying a large sex trait (Moller 1996); hence, *Tupinambis* males may benefit by increased body size.

Few studies have examined seasonal changes in dimorphism (Vitt and Cooper 1985) or addressed sexual characters as dynamic in relation to selective pressures. *Anolis* lizards with enlarged dewlaps tend to exhibit high bite forces, and a large dewlap is an important trait for polygynous lizards that often bite one another during male encounters (Vanhooydonck et al. 2005a, b). Irschick et al. (2006) indicated that head shape in green anoles remained constant across seasons, but bite force and dewlap changed. In *Tupinambis*, we observed that the variability in jaw muscle is associated with a temporal pattern in males. In addition, we observed males with increased muscle mass in the breeding season. According to Moller (1996), males may reduce the maintenance costs of secondary sexual characters by simply moulting those traits when they are not necessary. Based on our results, we highlight the importance of considering secondary sexual characters as dynamic traits because sexual selection would act not only by changing the size of the structure but also by adjusting the period of increased expression of the jaw muscle.

Signals are behavioural or morphological traits that influence other individuals (Henningesen and Irschick 2012); however, exploring what information is conveyed within a signal is a major challenge. For instance, in male green anoles the size of the dewlap is positively correlated with bite force, suggesting that it is a reliable signal (Vanhooydonck et al. 2005b; Irschick et al. 2006). Sexually active males of *Tupinambis* showed greater pterygoideus muscle mass than mature males without sperm in epididymides, independently of body size. Moreover, we found that sexually active males that had greater jaw muscle mass also had a greater testes mass. In *Tupinambis merianae* males in captivity, testosterone levels were found to be associated with reproductive activity (Chamut et al. 2012). Huyghe et al. (2010) showed that an increase in testosterone in *Gallotia galloti* caused an increase in jaw adductor muscle mass, without affecting bite force, however this muscle is situated at the side of the head, the muscle function may have become a visual signal (Herrel et al.



1999). Another explanation for the function of male sexual characters proposes that they advertise not only competitive ability, but also ejaculate quality (Sheldon 1994; Malo et al. 2005). We suggest that in *Tupinambis*, pterygoideus muscle may act as a signal of male quality because it is associated with the presence of sperm and testis size.

A male-biased sex ratio usually leads to increased intensity of sexual selection due to a greater competition among males, and often to strong mate choice in females (Clutton-Brock and Vincent 1991; Kvarnemo and Merilaita 2006). In *T. rufescens*, with a more male-biased sex ratio than *T. merianae*, the high intrasexual competition may be expected to lead to a greater increment in muscle mass in sexually active males than in *T. merianae*. However, our results show no difference in pterygoideus muscle mass of sexually active males between species, probably because sexual characters can be influenced not only by sex ratio but also by sexual differences in body size. Species like *T. merianae*, with less sexual body size dimorphism, are more likely to have intersexual pressures than species with marked sexual body size dimorphism, because males would need more force for grasping females during copulation. *Tupinambis merianae* and *T. rufescens* are different in sex ratio and sexual size dimorphism; however, they exhibit similar sexual dimorphism patterns of the jaw muscle (a sexually dimorphic and seasonal trait). Although sexual dimorphism of the jaw muscle could be a conservative trait in these closely related species, in *T. merianae*, muscle could be influenced mainly by intersexual pressures, whereas in *T. rufescens* the same character may be influenced by intrasexual competition.

To conclude, our results show that there is a significant positive correlation between muscle and testis mass; moreover, the increase in jaw muscle mass is associated with sperm presence, suggesting that the relative size of jaw muscle acts as an honest signal of reproductive condition of males. Furthermore, examining secondary sexual trait expression considering temporal processes proves helpful for understanding the factors shaping the processes of sexual selection.

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**Ethical standards** The authors declare that this paper comply with the current laws of Argentina.

**Conflict of interest** The authors declare that they have no conflict of interest.

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