

Phenotypic diversity and its relationship to reproductive potential in changing social contexts in a lizard model

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Phenotype in lizards is related to reproductive function, and hence to reproductive output. Besides the intraspecific diversity in phenotypes, their temporal variation throughout the reproductive season in relation to the variation of social contexts builds extra complexity into sexual selection scenarios. One useful model for understanding phenotypic diversity dynamics is *Tropidurus spinulosus* because it presents sexual dimorphism in different phenotypic traits, dichromatism in regions related to reproductive behaviour, and it has intense social reproductive interactions. We aimed to evaluate how the reproductive and phenotypic traits of individuals vary with changing social contexts, and how intrasexual phenotypic diversity and reproductive potential are explained by the phenotypic traits. In this study, we used data obtained during four consecutive breeding seasons (2015–2018) in a wild population. The social context, characterized according to the operational sex ratio, varied between months and, therefore, some phenotypic and reproductive traits also varied. We found that body robustness and chromatic diversity were the main sources of phenotypic diversity and were related to reproductive traits in both sexes. Our results help to understand the dynamics and reproductive implications of phenotypic diversity in changing social contexts in a lizard social model.

ADDITIONAL KEYWORDS: chromatism – dimorphism – reproductive traits – social contexts – temporal variations.

INTRODUCTION

Intraspecific phenotypic diversity has evolutionary importance since it means that different phenotypes are visible for selection within a species (Lee, 2011; Shine *et al.*, 2011). Phenotype is often related to the reproductive function of an organism, and hence to its microevolutionary fitness (Brown & Shine, 2005; Vergara *et al.*, 2012; Ward-Fear, 2016). Sexual selection thus benefits those phenotypic traits that maximize the reproductive potential, shaping reproductive strategies associated to morphs (Calsbeek *et al.*, 2010). Consequently, understanding the meaning of intraspecific phenotypic diversity in terms of reproductive potential is a current challenge of evolutionary ecology.

Besides intraspecific phenotypic diversity itself, its temporal variation throughout a reproductive season builds extra complexity into sexual selection scenarios. Reproductive strategies may be influenced by the intensity of sexual selection, which is modulated by changing social contexts (Kvarnermo & Simmons, 2013). Therefore, understanding phenotypic diversity dynamics requires exploring temporal variations of phenotypic and reproductive traits in relation to variations of the social contexts. Variations in the operational sex ratio (OSR), that is the proportion of males and females qualified to mate in a given period (Kvarnermo & Ahnesjö, 2002; Kvaneremo & Simmons, 2013), are useful to characterize changing social contexts. This parameter can be interpreted as the temporal and spatial availability of the mating resource; therefore, a deviation in the operational sex ratio can affect the intensity of sexual selection, leading to greater variability in the reproductive

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success of the individuals of the most abundant sex (Duvall *et al.*, 1992).

Species that have evolved towards sexual dimorphism are keys to understanding the evolution of phenotypic traits and their correlation with reproductive success according to social contexts. Sexual dimorphism, either in body size (Gienger & Beck 2007) or in the relative size of different body parts (e.g. abdomen, tail, head), can indicate the selective pressures imposed (Butler & Losos, 2002; Kratochvil *et al.*, 2003). Analysing how multiple dimorphic phenotypic traits of females and males are related to reproductive potential traits helps to understand how the selective forces have acted differentially on each sex (Cox *et al.*, 2003; Corl *et al.*, 2009). Phenotypic diversity associated with the reproduction of individuals may be explained by several independent traits that give rise to alternative non-discrete phenotypes (Cardozo *et al.*, 2015), and multiple trait selection better predicts reproductive success (Karsten *et al.*, 2009).

Body robustness measured through body condition indicates an animal's energy reserves, which are strongly associated with reproductive potential (Cardozo *et al.*, 2015; Falk *et al.*, 2017). Body condition, influenced by the amount of fatty substance stored, has been considered a reliable predictor of reproductive potential of individuals in many taxa within the Squamata (Bulte *et al.*, 2008; Cardozo & Chiaraviglio, 2008). Seasonal changes in body condition indicate that lipid storage has primarily reproductive purposes (Price *et al.*, 2017). In fact, abdominal fatty bodies in females release fatty acids that are converted into the phospholipid component of vitellogenin, the yolk precursor, which is the main source of energy for developing embryos (Price *et al.*, 2017).

Phenotypic traits, such as trunk length, abdominal volume and tail perimeter, could be important indicators determining the reproductive potential of female lizards. The width of the abdomen or the length of the trunk can limit the number of eggs to be developed by a female (Boretto & Ibarguengoytia, 2009; Bastiaans *et al.*, 2013; Scharf & Meiri, 2013). In addition, variations in tail perimeter in some species have been associated with the reproductive cycle (Cardozo *et al.*, 2015). The tail has large fatty deposits (Paz, 2016), distributed around the caudal vertebrae, as well as subcutaneously in its proximal section (Russell *et al.*, 2015).

In male lizards, variation in body size and in other phenotypic traits as well as in gonadal investment may be related to reproductive strategies (Dial *et al.*, 2008). Body size can be advantageous to obtain mates as a reproductive quality signal for females (Olsson, 1993). Male head size may be fundamental in intersexual interactions, such as female subjection during

copulation, as well as in intrasexual interactions such as agonistic encounters (Gvozdk & Van Damme, 2003). Tail perimeter, as mentioned above, could contribute energy resources to high-demand male behaviours, such as partner search, fighting and copulation (Gienger & Beck, 2007; Vitt & Cadwell, 2009).

Besides morphological dimorphism, chromatism is also subject to sexual pressure (García *et al.*, 2013). Colour pattern can function as an intra- and intersexual phenotypic signal of the individual's quality traits, such as body condition (Pérez i de Lanuza *et al.*, 2014), and thus be useful for being chosen as a partner and/or for giving signs to rivals (Olsson *et al.*, 2013). In some taxa, such as the Lacertidae and the Agamidae, the degree of dichromatism is positively associated with sexual size dimorphism (Pérez i de Lanuza *et al.*, 2013). In male lizards, the wide range of colours in body regions has been linked to reproductive displays (Rossi *et al.*, 2019). In female lizards, ventral coloration has been correlated with the individual's interactions, thus colouring may contribute to shape social relationships (Weiss, 2006; Vercken & Clobert, 2008). Moreover, the variability found in female throat coloration may be a signal in conspecific communication. Colour variations may reflect reproductive strategies (Gray & McKinnon, 2007) since they can be associated with phenotypic syndromes involving physiological, morphological and behavioural traits (Pérez i de Lanuza *et al.*, 2013). Therefore, understanding the relationship between colour patterns and reproductive potential is fundamental to elucidating the meaning of intraspecific colour diversity.

T. spinulosus is an interesting model because it is among the most dimorphic species of the family Tropicuridae (López Juri *et al.*, 2018a) and presents high sexual dichromatism and male-biased colour diversity which is involved in reproductive displays (Rossi *et al.*, 2019). Moreover, due to the intense social interactions observed in the field, we might expect variability in reproductive strategies.

To determine the dynamics and reproductive meaning of the intrasexual phenotypic diversity in our lizard model, we aimed to evaluate: (i) how reproductive potential and phenotypic traits of individuals (chromatic and sexually morphological dimorphic) vary with the changing social contexts, determined by temporal variations in the intensity of sexual selection; and (ii) how intrasexual phenotypic diversity and reproductive potential are explained by the phenotypic traits. We expected to find that phenotypic diversity of females and males reflect diversity in reproductive strategies, varying according to operational sex ratio, and that sexually dimorphic traits correlate with reproductive potential variables, including fat storage and gonadal investment.

MATERIAL & METHODS

SPECIES AND STUDY AREA

We captured *T. spinulosus* individuals in Tanti, Córdoba Province, Argentina (31°23'33"W, 64°35'48"S), corresponding to the phytogeographic region of Chaco mountain forest (Zak *et al.*, 2004). We recorded the capture sites with GPS and thus, after the laboratory studies, the specimens were released at their original site. The government environmental agency, Secretaría de Ambiente y Cambio Climático, gave us authorization for the scientific capture (Permit Numbers: 629892 053 815; 911312 053 416; 546833 053 717; 913508 053 318; 646238 053 119). This study was approved by the Ethics Committee of the Instituto de Diversidad y Ecología Animal CONICET-UNC (protocol number: 2/2017).

We used a line-transect method for field sampling (McDiarmid *et al.*, 2012). Transects were placed randomly and sufficiently far apart (~150 m) to avoid visiting the same sampling area. Such distance was markedly higher than the distance travelled by individual lizards (Ribeiro *et al.*, 2009). We did not repeat transects among field trips within a breeding season, nor among years, thus avoiding the resample of the same lizards. To carry out a representative and repeatable sampling, we standardized the sampling effort and avoided bias according to Kenett Dodd (2016): (i) we sampled the study population regularly (twice a month, every month); (ii) the sampled areas were equivalent in size in each survey; (iii) all surveys were carried out by trained observers.

We collected mature individuals during the breeding season (see López Juri *et al.*, 2018b) between August and December (2015–2018). According to the criterion of the smallest reproductive male and female (Madsen *et al.*, 2006), we determined that males and females reach sexual maturity at 82 mm SVL. To measure phenotypic (morphological and chromatic) and reproductive traits, we transported the lizards to the laboratory where we kept them in individual boxes (width 23 cm, length 34 cm and height 29 cm) at 25 °C and under a normal photoperiod (12 h light/12 h dark) with UVB light. The lizards were maintained at the laboratory for approximately 15 days with access to water and live food (crickets and mealworms) *ad libitum*.

MEASUREMENT OF PHENOTYPIC TRAITS

As we aimed to evaluate the phenotype of males and females during the mate search, we characterized the phenotype of the sexually receptive females ($N = 82$) and reproductive males ($N = 150$); excluding pregnant females ($N = 77$) (see the section Measurement of reproductive potential). We recorded the following

morphological traits: snout-vent length (SVL), trunk length (TL), abdominal perimeter (AP), tail perimeter (TP), head width (HW), and head height (HH), which were measured to the nearest 1 mm with a digital caliper. Body mass (BM) was recorded to the nearest 0.01 g with a digital balance (Traveler OHAUS; precision: 0.01 g).

To characterize the chromaticism of the individuals, we took lateral and ventral photographs under standardized lighting conditions (artificial fixed light, set manually: speed 1/60, aperture of the diaphragm 3.9, flash +0.3, and autofocus). The image in Figure 1 demarcates the body sectors studied in males (flanks, belly and throat) and females (throat). We selected these body regions because of their colour characteristics (dichromatism and colour variability) and their relation to intraspecific communication (Rossi *et al.*, 2019).

In previous studies, we characterized the dichromatic colours of the species from a lizard visual model using spectrophotometric data (Rossi *et al.*, 2019). In the flanks, the dichromatism was mainly due to male-specific light blue spectra reflected by the outer ventral scales together with medium-wavelength green and long-wavelength yellow spectra. In the belly and the throat of males, the dichromatism was mainly due to orange spectra. In females, the throat was less saturated than males but presented high variability in yellow chroma between individuals (N. Rossi, pers. obs.). Therefore, in this study, we quantified the following colours: blue, green and yellow in the flanks of males, orange in the belly and throat of males, and yellow in the throat of females. The extent of each colour was measured as a percentage of the area of each body region. We identified spectral

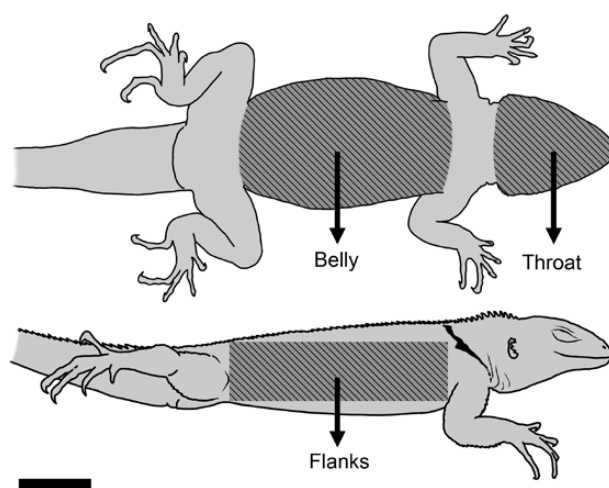


Figure 1. Scheme to demarcating the body sectors studied in males (flanks, belly and throat) and females (throat) of *T. spinulosus*.

signatures of each colour from pixels in pictures of ten individuals for each sex. All the individuals presented the dichromatic clusters mentioned above and were selected randomly according to Rossi *et al.* (2019). The number of pixels sampled was related to the area of the body regions: yellow: 691 pixels, green: 1163, blue: 1836, orange: 1682). We employed these pixels in a supervised classification, namely a cluster analysis, using the “Random Forest” algorithm of the homonym package in R (Liaw & Wiener, 2002). The algorithm partitioned the representative pixels into a training dataset and a test dataset which was used to validate the classification process. The validation yielded an out-of-bag error of 9% which is considered low (Millard & Richardson, 2015).

MEASUREMENT OF REPRODUCTIVE POTENTIAL

Body condition is an estimator of reproductive potential in both sexes (Bulte *et al.*, 2008), therefore we calculated residual scores from the general linear regression of ln-transformed body mass to SVL in sexually receptive females and reproductive males (Madsen & Shine, 2002; Bertona & Chiaraviglio, 2003). Furthermore, we evaluated reproductive condition by ultrasound scanning (portable Sonosite 180 Plus, transducer 5–10 MHz) (Cardozo & Chiaraviglio, 2008). Females were considered reproductive if they had vitellogenic follicles bigger than 5 mm diameter or oviductal eggs (López Juri *et al.*, 2018b). Reproductive females were distinguished in two categories: receptive and pregnant. Females with ovarian follicles (hyperechogenic aspect and diameter range: 5–14 mm) were classified as sexually receptive ($N = 82$). Females with oviductal eggs (with thickened and laminar edges and diameter > 14 mm) were classified as pregnant. Females captured pregnant from the field and females that at the end of the laboratory stay showed signs of pregnancy by ultrasound scanning (possible due to previous copulae in the field) (in total $N = 77$) were maintained in captivity until oviposition in order to estimate reproductive potential based on Clutch Size (CS) (number of oviposited eggs). Males were classified as reproductive if they had enlarged testes (hyperechogenic aspect and testicular width range: 5–10 mm) and presented semen (López Juri *et al.*, 2018c: see electrostimulation protocol) ($N = 150$). Reproductive potential was calculated as the testicular volume using the equation for an ellipsoid (Méndez & Villagrán, 1998).

SOCIAL CONTEXT CHARACTERIZATION

The social contexts were characterized according to the intensity of sexual selection, measured as operational sex ratio (OSR). To determine the OSR we calculated the ratio of reproductive males with sperm to sexually

receptive females with vitellogenic follicles (OSR was expressed as males: females). To evaluate temporal variations in the intensity of sexual selection during the reproductive season, we calculated the OSR each month. For OSR, we used the pooled data from two breeding seasons (2015 and 2016); the effect of year on the monthly variation of OSR was previously considered according to statistical analyses. We then evaluated the monthly variations of phenotypic (morphological and chromatic) and reproductive potential traits, to determine relationships with the OSR variations.

STATISTICAL ANALYSES

Two researchers measured the morphological and reproductive traits (G.L.J. and N.R.). The researcher as a random effect was always significant, so we applied linear mixed models.

To determine the sexual dimorphism of the species, we examined the effect of sex on body size. In the other morphological traits (TL, AP, TP, HW and HH), we examined the effect of sex adding the effect of body size.

To quantify the investment in each phenotypic (morphological and chromatic) and reproductive trait, we obtained the residuals of the regression between each variable and the SVL in each sex (Melville & Swain, 2000; Cardozo *et al.*, 2015). We thus obtained the following indexes: (i) morphological variables: Resi_TL (residue trunk-length); Resi_AP (residue abdominal perimeter); Resi_TP (residue tail perimeter); Resi_HW (residue head width); (ii) chromatic variables: Resi_yellow_throat_area (residue yellow throat area); Resi_blue_flank_area (residue blue flank area); Resi_green_flank_area (residue green flank area); Resi_yellow_flank_area (residue yellow flank area); Resi_orange_belly_area (residue orange belly area); Resi_orange_throat_area (residue orange throat area); (iii) reproductive variables: Resi_TV (residue testicular volume); Resi_CS (residue clutch size).

We used a Cochran–Mantel–Haenszel test (Agresti, 2002) to check if there was an effect of year on the monthly variation of OSR. We did not find any effect (Cochran–Mantel–Haenszel $M^2 = 7.49$; $df = 4$; $P = 0.11$), thus we pooled data across years. To compare the OSR between months throughout the breeding season, we performed a Chi-square test. To know if phenotypic (morphological and chromatic) and reproductive traits vary temporally, we applied linear mixed models to examine the effect of months on such traits using the Wald Chi-square test. Covariation between phenotypic and reproductive traits was tested using a Pearson correlation test.

To explore from a multivariate perspective how phenotypic variables explain phenotypic diversity, and also the association between phenotypic and reproductive traits, we applied principal component

analysis (PCA). Moreover, we evaluated monthly variations in phenotypic and reproductive traits with MANOVA, using the scores on the first and second principal components. An *a posteriori* Hotelling's test was also performed.

To know which phenotypic variables best explain reproductive potential, we examined the effects of themorphological and chromatic traits on body condition, Resi_CS and Resi_TV. In the case of Resi_CS we tested if such variable was related to the female phenotypic traits that had been measured initially when females had been receptive ($N = 41$). Then, we carried out the Selection of the Best Model using the Akaike information criterion (AIC) and Δ_i , where the model with the lowest AIC index is considered the most appropriate, and the models in which the difference in the AIC relative to the lowest AIC is < 2 can also be considered explanatory (Anderson *et al.*, 1994; Lorenzon *et al.*, 2001). We also used the Akaike weights statistic as evidence of the weight of each model, indicating the probability that a given model is the best among a series of candidate models (Burnham & Anderson, 2004).

We conducted all tests in R v.3.4.1 (R Core Team, 2017).

RESULTS

T. spinulosus presented sexual dimorphism in body size, with males being larger than females (Female SVL = 97.21 ± 0.94 cm; Male SVL = 115.74 ± 0.70 cm; ANOVA: $F = 247.18$; $df = 1$; $P < 0.01$). Other phenotypic traits related to reproduction were also sexually dimorphic, some being male-biased (TP and HW), and others female-biased (TL and AP) (Table 1).

The social context, characterized by the OSR, varied monthly throughout the breeding season (Fig. 2)

(Chi-square test: $\chi^2 = 11.48$; $P = 0.02$). In August and September, OSR was more balanced between sexes than in October, November and December when it was markedly male-biased.

In females, body condition and clutch size varied among reproductive months (Body Condition: Wald Chi-Square = 11.53, $P = 0.02$; Resi_CS: Wald Chi-Square = 3.78, $P < 0.01$). At the beginning of the breeding season, females presented high body condition, and relative clutch size was highest in November (Fig. 3) (raw data of number of oviposited eggs: mean \pm SD: October = 5.86 ± 1.07 ; November = 5.79 ± 1.14 ; December = 5.46 ± 1.27 ; January = 4.60 ± 0.97). Also, yellow throat area of females varied among months (Resi_yellow_throat_area: Wald Chi-Square = 13.77, $P < 0.01$) (Fig. 3), covarying negatively with body condition (Resi_yellow_throat_area: $r = -0.30$, $P < 0.01$). Trunk length and abdominal perimeter did not vary significantly in univariate analysis (Resi_TL: Wald Chi-Square = 3.18, $P = 0.52$; Resi_AP: Wald Chi-Square = 6.39, $P = 0.17$).

In males, body condition and testicular volume varied among reproductive months (Body Condition: Wald Chi-Square = 46.73, $P < 0.01$; Resi_TV: Wald Chi-Square = 33.05, $P < 0.01$) (Fig. 3). Tail perimeter and head width of males also varied among months (Resi_TP: Wald Chi-Square = 23.80, $P < 0.01$; Resi_HW: Wald Chi-Square = 28.37, $P < 0.01$) (Fig. 3). Tail perimeter covaried positively with body condition (Resi_TP: $r = 0.53$, $P < 0.01$) and testicular volume (Resi_TP: $r = 0.25$, $P = 0.01$). Head width also covaried positively with body condition but less closely than tail perimeter (Resi_HW: $r = 0.20$, $P = 0.01$). Blue colour area on the males' flanks varied among months (Resi_blue_flank_area: Wald Chi-Square = 12.85, $P = 0.01$) (Fig. 3), covarying negatively with their body condition (Resi_blue_flank_area: $r = -0.18$, $P = 0.04$). Other

Table 1. Sexual dimorphism in phenotypic traits of *T. spinulosus*

Traits	Sex	ANCOVA mean Aj (mm)	SE	F (sex)	<i>P</i>	F (SVL covariate)	<i>P</i>
TL	M	51.30	1.99	35.46	< 0.001*	1263.24	< 0.0001*
	F	53.55	1.99				
TP	M	50.67	2.70	44.61	< 0.0001*	378.379	< 0.0001*
	F	46.67	2.62				
AP	M	83.26	1.66	28.36	< 0.0001*	590.020	< 0.0001*
	F	87.50	1.71				
HH	M	13.02	0.39	1.34	0.2483	315.338	< 0.0001*
	F	12.84	0.40				
HW	M	21.31	0.86	22.43	< 0.0001*	695.017	< 0.0001*
	F	20.52	0.86				

*ANCOVA Mean Aj: Adjusted mean; SE: Standard error; TL: trunk length; TP: tail perimeter; AP: abdominal perimeter; HH: head height; HW: head width. Reproductive males $N = 150$, Receptive females $N = 82$.

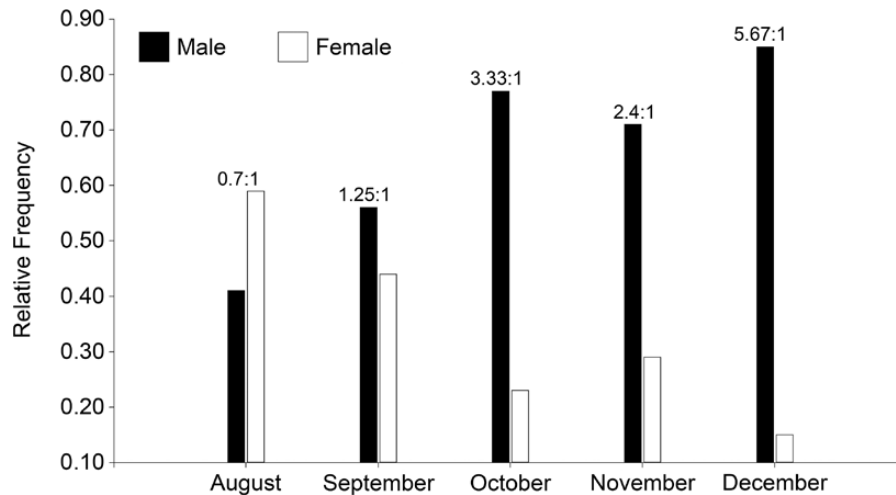


Figure 2. Dynamics of the OSR during the breeding season of *T. spinulosus* ($N = 127$) (Relative frequency of receptive females and reproductive males is represented on the y-axis; OSR values are indicated over the bars) (Reproductive Males: August $N = 7$, September $N = 10$, October $N = 30$, November $N = 24$, December $N = 17$; Receptive Females: August $N = 10$, September $N = 8$, October $N = 9$, November $N = 9$, December $N = 3$).

male phenotypic traits did not vary significantly in univariate analysis (SVL: Wald Chi-Square = 2.51, $P = 0.64$; Resi_green_flank_area: Wald Chi-Square = 7.25, $P = 0.12$; Resi_yellow_flank_area: Wald Chi-Square = 6.39, $P = 0.17$; Resi_orange_belly_area: Wald Chi-Square = 5.99, $P = 0.20$; Resi_orange_throat_area: Wald Chi-Square = 3.62, $P = 0.46$).

Using PCA, we analysed the phenotypic and reproductive variation integrally. In sexually receptive females, the most phenotypic variation (PC1) was found in body condition and in abdominal perimeter (Fig. 4; Table 2). Trunk length and yellow throat area (PC2) correlated inversely. According to PC1 and PC2 scores, reproductive and phenotypic variation presented a temporal dynamic (ANOVA month effect PC1: $F = 2.55$, $P = 0.04$; PC2: $F = 2.83$, $P = 0.03$). Sexually receptive females at the beginning of the breeding season presented a whiter throat and longer trunk, and were more robust than females in the late season.

In males, the most phenotypic variation was found in body condition and in tail perimeter inversely correlated with green and blue flank area and with head width (PC1) (Fig. 5; Table 3). Orange area in throat and belly, and yellow flank area as well as testicular volume (PC2) all correlated with each other. According to PC1 scores, reproductive and phenotypic variation showed a temporal dynamic (ANOVA month effect, PC1: $F = 9.85$, $P = 0.01$). Reproductive males presented higher body condition, testicular volume, tail perimeter and yellow flank area early in the breeding season than late in the season. In contrast they had larger green and blue flank areas and a more

robust head late in the breeding season than early in the season.

The multivariate models that best predicted female body condition included abdominal perimeter, and yellow throat area as predictors (Resi_AP: $F = 76.21$, $P < 0.01$; Resi_yellow_throat_area $F = 7.54$, $P = 0.01$; First multiple regression model: $R^2_{Aj} = 0.56$; Table 4), and the models that best predicted clutch size included trunk length and abdominal perimeter as predictors, although no significance was found (Resi_TL: $F = 2.19$, $P = 0.15$; Resi_AP: $F = 2.58$, $P = 0.12$; First multiple regression model: $R^2_{Aj} = 0.20$; Table 5).

In males, the multivariate models that best predicted body condition included tail perimeter and head width as predictors (Resi_TP: $F = 82.78$, $P < 0.01$; Resi_HW: $F = 57.72$, $P < 0.01$; First multiple regression model: $R^2_{Aj} = 0.48$; Table 6), and the models that best predicted testicular volume included tail perimeter and yellow flank area as predictors (Resi_TP: $F = 3.03$, $P = 0.01$; Resi_yellow_flank_area: $F = 2.71$, $P = 0.01$) (First multiple regression model: $R^2_{Aj} = 0.20$) (Table 7).

DISCUSSION

Our results in a lizard model help to understand the dynamics and reproductive meaning of phenotypic diversity in changing social contexts. Certain phenotypic traits in *T. spinulosus* are related to variation in reproductive investment. Moreover, changes in reproductive and phenotypic traits in association with OSR show that temporal trait variation builds complexity into sexual selection scenarios. Males

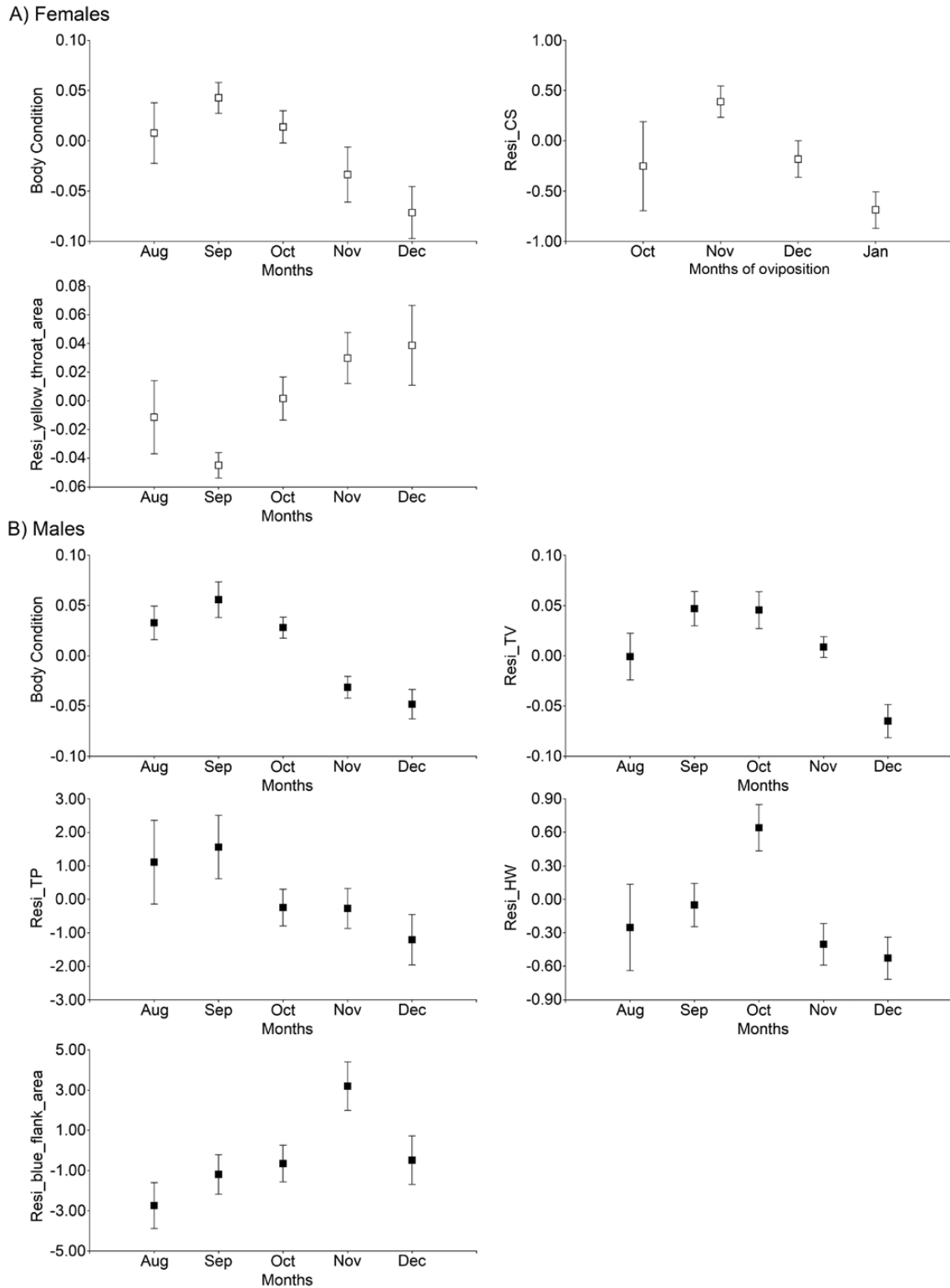


Figure 3. Dynamics of reproductive and phenotypic traits of *T. spinulosus* in (A) receptive females (Resi_CS: residue clutch size, Resi_yellow_throat_area: residue yellow throat area; Body condition $N = 82$, for Resi_yellow_throat_area $N = 73$, for Resi_CS $N = 77$); (B) reproductive males (Resi_TV: residue testicular volume, Resi_TP: residue tail perimeter, Resi_HW: residue head width; Body condition $N = 150$, Resi_TV $N = 129$, Resi_TP $N = 150$, Resi_HW $N = 150$, Resi_blue_flank_area $N = 127$). Only traits that presented significant differences between months are represented. Graphs show mean value and SE.

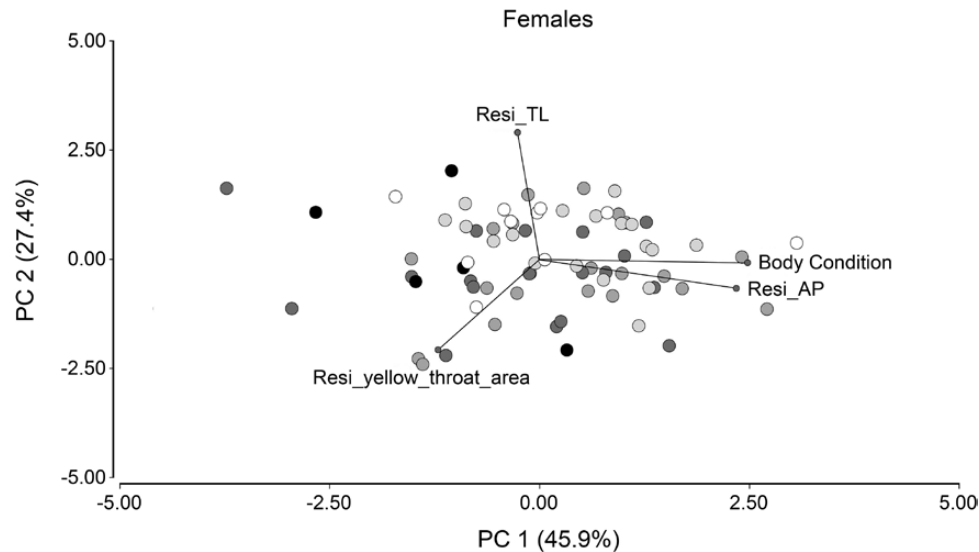


Figure 4. PCA relating reproductive and phenotypic traits in receptive females of *T. spinulosus* among months (August: white, September: light grey, October: medium grey, November: dark grey, December: black; $N = 73$).

and females had different reproductive potential throughout the breeding season which was reflected in their phenotype, thus shaping dynamic reproductive strategies within a population.

T. spinulosus showed that sexual selection has led to sexual dimorphism, but sex-bias varies in the different body traits. Males have greater body size than females, not only in body length but also in head and tail robustness. Conversely in receptive females, trunk length and abdominal perimeter were exacerbated. Moreover, we found that, besides being dimorphic, morphological traits are integrated, giving rise to phenotypes that correlate with the reproductive investment of individuals.

In females, the phenotypic variables that explained reproductive potential, either as body condition or clutch size, were the dimorphic female-biased traits, i.e. trunk length and abdominal perimeter. The association between abdomen robustness and body condition reflects abdominal fat storage (Boretto & Ibarraengoytia, 2009; Cardozo *et al.*, 2015). Such storage may facilitate high energy-cost processes involved in reproduction, for example, reproductive thermoregulation processes. Reproductive females with wide abdominal perimeter and high body condition are able to maintain thermal stability, which would be beneficial for reproduction (López Juri *et al.*, 2018b). Fat storage in abdominal bodies is also an energy source for the development of ovarian follicles and oviductal eggs (Ramirez Bautista & Olvera Becerril, 2004; Price *et al.*, 2017). Furthermore, we found that abdomen robustness and trunk length were correlated with investment in clutch size. As

the abdomen physically limits the offspring, its size is under direct selection pressure (Stuart-Fox, 2009). Concordantly, in a macroevolutionary comparison across taxa, López Juri *et al.* (2018a) showed that the evolution of a large abdomen allows females to accommodate more offspring.

In males, the phenotypic variables that explained reproductive potential, either as body condition or as testicular volume, were the dimorphic male-biased traits, i.e. head width and tail perimeter. The association between head robustness and fat storage suggests that an increase in head size can be concomitant with high energy cost activities (Gvozdik & Van Damme, 2003). The robustness of the head is important during intercourse when the male holds the female in the back of the neck (Pough *et al.*, 2001), or also in aggressive intra-sexual interactions where the muscle mass of the head can determine success against rivals (Husak *et al.*, 2006; Naretto *et al.*, 2014). The proximal section of the tail allows fat storage (Cardozo *et al.*, 2015), which is allocated for the search for a partner, intercourse and fights between males (Gienger & Beck, 2007; Vitt & Caldwell, 2009).

Our results also indicate that morphological combined with chromatic traits give information about the individual's reproductive quality. In males, tail robustness in association with the yellow flank area was correlated with investment in testicular volume. Robustness of certain body parts has already been characterized as an honest signal when associated with testicular size in other lizard models (e.g. Naretto *et al.*, 2016). However,

our interesting novel finding concerns chromatic messages. *T. spinulosus* is a lizard with a variety of colours arranged in complex patterns (Rossi *et al.*, 2019). We detected, however, that the yellow colour of the flanks is the only chroma associated with male reproductive potential. Yellow scales on the flanks would function as a visual signal, similarly to the Agamidae, in which the extent of yellow pigmentation on the flanks has been correlated with indices of sexual selection (Chen *et al.*, 2013). Previous studies in *T. spinulosus* have demonstrated that yellow scales spatially close to green scales constitute a similar pattern to the nuptial coloration of *Lacerta viridis* (Molnar *et al.*, 2013; Rossi *et al.* 2019). The coordinated dynamics in coloration and testicular volume, probably regulated by sex steroid hormones (Calisi & Hews, 2007), may be advantageous by reducing costly exhibits during courtship and copulation (Cooper & Greenberg,

1992). Therefore, the robustness of dimorphic morphological traits together with yellow specific chroma would act as a sign of male quality because of their association with male reproductive potential (body condition and testicular volume).

Sexual dimorphism has often arisen from unbalanced sexual selection pressures imposed on the sexes (Butler & Losos, 2002; Kratochvil *et al.*, 2003). Thus, if sexual pressures change during the breeding season, it is to be expected that individuals with certain traits will be more favored than others, according to the intensity of sexual selection operating. Thus, temporal-related variations in the phenotypic composition of the reproductive population would be frequent. In our study, OSR changed temporally, accentuating male competition in the mid-late breeding season. Concordantly tail perimeter and head width of males were marked dynamic traits that varied in relation to OSR changes and to testicular volume and body condition. In females, yellow throat area was also a dynamic trait that increased at the end of the reproductive season and correlated inversely with female fat reserves. We could not assert if such dynamics were due to changes that occurred in individual lizards over the course of a reproductive season or due to variation in lizards that reproduced early vs. late in the season. Traits related to chroma and robustness might be plastic in an individual, however, structural traits like body size are more fixed. Anyway, these concomitant changes in reproductive and phenotypic traits occurring in changing OSR scenarios suggest that

Table 2. Loadings of reproductive and phenotypic traits on principal components in receptive females of *T. spinulosus*

	PC1*	PC2
Body condition	0.68	-0.02
Resi_TL	-0.07	0.8
Resi_AP	0.65	-0.18
Resi_yellow_throat_area	-0.33	-0.57

*PC1: First Principal Component; PC2: Second Principal Component; Resi_TL: residue trunk length, Resi_AP: residue abdominal perimeter, Resi_yellow_throat_area: residue yellow throat area; N = 73.

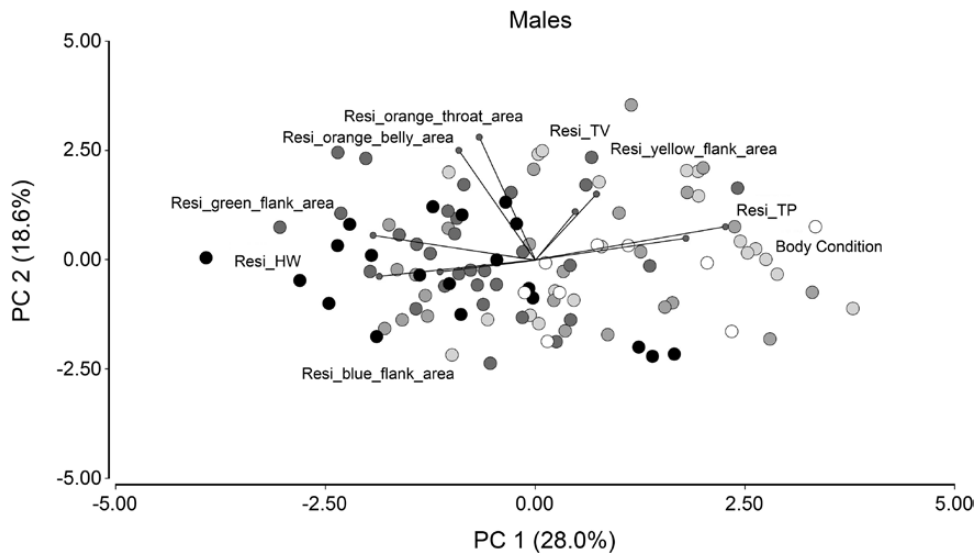


Figure 5. PCA relating reproductive and phenotypic traits in reproductive males of *T. spinulosus* among months (August: white, September: light grey, October: medium grey, November: dark grey, December: black; N = 104).

the pressure of sexual selection imposes temporal variations, phasing reproductive strategies within a population.

As mentioned above, at the beginning of the breeding season, females presented high body condition but small yellow throat area. This optimal body condition is to be expected, because individuals often store lipids from the summer until winter, and thus in late winter they have entire fat reserves to be allocated to follicular growth (Ortiz *et al.*, 2014). Regarding the color of the throat region, Rossi *et al.*, (2019) observed that the ventral regions of females produce high stimulation of UV cones in conspecifics. Specifically, the white throat that characterizes female coloration is UV-rich, whereas long wavelengths, e.g. yellow pigmentation, are UV-poor. In other lizard species, such as *Ctenophorus ornatus*, UV-chroma often correlates with sexual receptivity and is highly selected by males (Lebas & Marshall, 2000). Consequently, the white throat of females at the beginning of the breeding

season, in conjunction with a high body condition score, could function as a condition-dependent reproductive signal (Weiss *et al.*, 2006), indicating high reproductive potential.

It would be interesting to know if clutch size of lizard females might be related to female colour. An strong relationship between female colour morphs and clutch size has been found in some species such as *Podarcis muralis* (Pellitteri-Rosa, 2012), *Uta stansburiana* (Sinervo & Lively, 1996) and *Lacerta vivipara* (Sinervo *et al.*, 2001). We could not analytically detect a close correlation between clutch size and throat colour of females when they were sexually receptive. However, using the criterion that the time to produce one clutch corresponds to the period between the first female with vitellogenic follicles and the first female with corpora lutea (Galdino *et al.*, 2003; Ortiz *et al.*, 2014), our results suggest that females that presented high clutch size (November) correspond to the receptive females with marked white throat and high body condition (September).

In males, sexual pressures change might influence reproductive and phenotypic traits throughout the reproductive season. At the beginning, males appeared with optimal body condition, high testis investment, and robust tail and head. As expected, yellow chroma correlated dynamically with testicular volume, reflecting male reproductive potential. However, we found that these early reproductive males had a small area of short wavelength blue on the flanks, although the dichromatism in this species is mainly due to these wavelengths located in the outer ventral scales (together with medium-wavelength green and long-wavelength yellow spectra; Rossi *et al.*, 2019). In species such as *Podarcis muralis*, blue is an important signal for conspecifics during the breeding season (Perez i Lanuza & Font, 2015), which can be exhibited to opponents during lateral circulation displays (Rossi *et al.*, 2019). Our results indicate that the blue flank area increases toward the mid-late reproductive season when OSR is highly biased to males, accentuating male-male competition. Further studies are needed to test if

Table 3. Loadings of reproductive and phenotypic traits on principal components in reproductive males of *T. spinulosus*

	PC1*	PC2
Body condition	0.41	0.11
Resi_TV	0.17	0.34
Resi_TP	0.52	0.17
Resi_HW	-0.26	-0.06
Resi_yellow_flank_area	0.11	0.25
Resi_blue_flank_area	-0.43	-0.09
Resi_green_flank_area	-0.44	0.13
Resi_orange_throat_area	-0.21	0.57
Resi_orange_belly_area	-0.15	0.64

*PC1: First Principal Component; PC2: Second Principal Component; Resi_TV: residue testicular volume, Resi_TP: residue tail perimeter, Resi_HW: residue head width, Resi_yellow_flank_area: residue yellow flank area, Resi_green_flank_area: residue green flank area, Resi_blue_flank_area: residue blue flank area, Resi_orange_throat_area: residue orange throat area, Resi_orange_belly_area: residue orange belly area; $N = 104$.

Table 4. Relationship between body condition and phenotypic traits considering the best multiple regression models in receptive females of *T. spinulosus*

Model	AICc*	Δ_i	Wi	Independent variables	Slope
Body condition ~ Resi_AP	-160.4	0.00	0.670	Resi_AP†	0.1442
Body condition ~ Resi_AP + Resi_yellow_throat_area	-158.9	1.49	0.317	Resi_AP Resi_yellow_throat_area	0.1388 -0.0437

*AICc: Akaike information criterion; Δ_i : Akaike differences; Wi: Akaike weights.

†Resi_AP: residue abdominal perimeter; Resi_yellow_throat_area: residue yellow throat area; $N = 73$.

Table 5. Relationship between clutch size and phenotypic traits measured previously when females were receptive, considering the best multiple regression models in females of *T. spinulosus*

Model	AICc*	Δi	Wi	Independent variables	Slope
Resi_CS ~ Resi_AP	130.1	0.00	0.336	Resi_AP†	0.6921
Resi_CS ~ Resi_TL	130.6	0.49	0.263	Resi_TL	0.6335
Resi_CS ~ Resi_TL + Resi_AP	131.0	0.91	0.213	Resi_TL Resi_AP	0.5028 0.5403

*AICc: Akaike information criterion; Δi : Akaike differences; Wi: Akaike weights.

†Resi_CS: residue clutch size, Resi_TL: residue trunk length, Resi_AP: residue abdominal perimeter; $N = 41$.

Table 6. Relationship between body condition and phenotypic traits considering the best multiple regression models in reproductive males of *T. spinulosus*

Model	AICc*	Δi	Wi	Independent variables	Slope
Body condition ~ Resi_TP + Resi_HW	-324.4	0.00	0.913	Resi_TP† Resi_HW	0.1195 0.0932

*AICc: Akaike information criterion; Δi : Akaike differences; Wi: Akaike weights.

†Resi_TP: residue tail perimeter, Resi_HW: residue head width; $N = 150$.

Table 7. Relationship between testicular volume and phenotypic traits considering multiple regression models in reproductive males of *T. spinulosus*

Model	AICc*	Δi	Wi	Independent variables	Slope
Resi_TV† ~ Resi_TP	-194.9	0.00	0.323	Resi_TP	0.0795
Resi_TV ~ Resi_TP + Resi_Yellow_flank_area	-193.4	1.44	0.157	Resi_TP Resi_Yellow_flank_area	0.0731 0.0444
Resi_TV ~ Resi_Yellow_flank_area	-193.2	1.68	0.139	Resi_Yellow_flank_area	0.0491

*AICc: Akaike information criterion; Δi : Akaike differences; Wi: Akaike weights.

†Resi_TV: residue testicular volume; Resi_TP: residue tail perimeter; $N = 129$.

the blue area is related to the individual competitive ability of males.

According to our results, synchronized changes in reproductive and phenotypic traits are fundamental to understanding the temporal variation of reproductive strategies. The temporal phasing of reproductive and phenotypic traits in close relation to changes in OSR may be related to changes in the intensity of pre- and postcopulatory sexual selection (Devigili *et al.*, 2013; Blengini *et al.*, 2016). At the beginning of the breeding season in our model, when OSR was balanced and high-quality reproductive females (high body condition and high clutch size) were abundant, males invested preferably in testis mass. High testicular volume could be related to the postcopulatory strategy, since the proportion of sperm allocated often correlates positively with female quality, according to Reinhold *et al.* (2002). López Juri (2019) found that sperm parameters are related to the dimorphic trait SVL; however, in future studies we need to test if sperm performances vary

according to changing social scenarios. On the other hand, when OSR was male-biased (which is positively related to mate aggression, see Weir *et al.*, 2011), males invested more in precopulatory weapons, such as head width and blue colour production, which may signal competitive ability to opponents.

PCA analyses support the above discussion, since they show that phenotypic variability is explained by the individual's robustness and energy reserves and as well as by some chroma components, and that such variability is temporally dynamic throughout the reproductive season. Females show little variation in linear traits (such as TL) but vary greatly in fat reserve and chromatic traits, as Cardozo *et al.* (2015) found in large lizards, such as *Salvator merianae*. In males, there is also great phenotypic variation in body robustness and colour diversity. Rossi *et al.* (2019) observed colour diversity in *T. spinulosus* in dichromatic regions such as the flanks, suggesting that sexual selection acts also on the complexity

of colour phenotypes. However, further studies of colour combination are needed, using visual models in relation to reproductive condition, and considering dynamic dichromatism (Rossi *et al.*, 2019).

In conclusion, our results indicate that sexually dimorphic phenotypic traits correlate with some reproductive traits and that both vary with social contexts, determined by the intensity of sexual selection. The phenotypic diversity of females and males that became reproductive within a season was dynamic and related to sexual selection scenarios, phasing temporal reproductive strategies according to operational sex ratio. This contributes to understanding the biological meaning of phenotypic variability, which is an important question in the field of evolutionary ecology.

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