New Insights into Bite Performance: Morphological Trade-Offs Underlying the Duration and Magnitude of Bite Force*

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ABSTRACT

Biting performance is important for feeding, territory defense, and mating in many animals. While maximal bite force is a well-studied trait, other aspects of biting and their variation depending on behavior are rarely considered. Here, we took an innovative approach, where (1) we quantified a novel trait, bite duration in lizards; (2) we examined variation across setups that simulate feeding and antagonistic behavior; and (3) we used F-matrix statistics to investigate how different functional components are optimized for ecological and social demands with respect to individual morphology. Our results did not show differences between the sexes in bite duration, but bite performance varied across experimental setups in males, suggesting a higher functional flexibility in this sex. The investigation of form-function associations revealed that trade-offs, facilitations, and one-to-one relationships are simultaneously involved in the morphological optimization of bite force and duration. Put together, our integrated analysis of two different components of bite performance—force and duration—demonstrates their importance for males in both ecological and social tasks. Our findings also suggest the existence of trade-offs in the morphological optimization of functional components, possibly due to physiological constraints on muscle composition, insertion, and orientation.

Keywords: head morphology, bite duration, bite force, behavior, F-matrix.

Introduction

The study of how morphology-function associations vary among animals when performing ecologically relevant tasks (e.g., capturing prey or escaping predators) can help us understand the selective pressures molding morphological diversity (Arnold 1983; Irschick 2002). Natural and sexual selection shape phenotypic variation across individuals (Endler 1984; Ryan and Rand 1990; Vincent and Herrel 2007), but the relative contribution of each is not always easy to determine (Herrel et al. 1999*b*; Lopez-Darias et al. 2015). Indeed, the different social roles of male and female individuals of a population may impose different evolutionary pressures on the members of each sex, particularly with respect to the balance between survival and reproduction (Andersson 1994; Jones and Ratterman 2009; Fritzsche and Arnqvist 2013). In many species, males compete for access to females and are territorial (Stamps 1983); thus, males have higher reproductive investment and are "choosier" (Jones and Ratterman 2009). This frequently brings about different functional demands for each sex, where males tend to be more active and aggressive, while females tend to be more cryptic. Ultimately, this may cause differences between the sexes in how they are exposed to the effect of natural selection (i.e., through resource acquisition and predator avoidance) and that of sexual selection (i.e., for fulfilling different social activities; Cunningham and Birkhead 1998).

Considering the balance between the evolutionary mechanisms involved, different functional needs may be difficult to optimize simultaneously because of conflicting demands within the same phenotypic trait. Individuals may perform several tasks fairly well but with none of them especially optimized. This trade-off between functional flexibility and performance excellence has been termed the "jack-of-all-trades-master-of-none" hypothesis (Tulli et al. 2012; Irschick and Higham 2016). Alternatively, individuals may become specialized in one task at the cost of performing suboptimally in another, which leads to functional specialization (Huey and Hertz 1984; Arnold 1992; Konuma and Chiba 2007; Herrel et al. 2009; Irschick and Higham 2016). A well-known example is the trade-off between speed and endurance in athletes, which exhibits a marked

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negative correlation when comparing professional sprinters and marathoners (Irschick and Higham 2016). Another well-known trade-off occurs between velocity and force. Fiddler crabs *Uca pugnax* use their claws both for fighting rivals and for feeding (Levinton and Allen 2005), and crabs with longer claws increase closing speed but exhibit lower pinching forces. In other words, crabs with one specific claw morphology cannot be quick and strong at the same time. The same is the case with the lever system of scorpion chela, where a functional trade-off between speed and force has been identified across species (Simone and van der Meijden 2017). Likewise, a trade-off between bite force and jaw velocity exists in Darwin's finches, where higher bite forces have been associated with slow beak movements (Herrel et al. 2009). Darwin's finches that have strong and robust beaks to crush harder seeds may be constrained in their vocal tract resonance function (Herrel et al. 2009). In this case, finch species can have robust beaks to crush harder seeds or instead have gracile beaks allowing them to produce complex song types.

Head morphology along with its association with bite performance and ecology is one of the most studied animal functional systems because of its central role in many basic activities (e.g., Dessem and Druzinsky 1992; Herrel et al. 1999*a*, 1999*b*; Dumont and Herrel 2003; Erickson et al. 2004; van der Meij and Bout 2004). Lizards are probably the most studied model organisms regarding the association between head morphology and bite force performance, which is highly relevant during social and ecological tasks, including feeding, mating, antipredator defense, male-male combat, and territorial contests. On one hand, sexual selection acts on bite force, which increases male potential for territorial and antagonistic behavior, yielding sexual dimorphism in biting performance and related morphological traits (Herrel et al. 1999*b*; Husak et al. 2006, 2009). On the other hand, natural selection may act to promote resource partitioning, where larger individuals may have the capacity to eat larger and/or harder prey as a result of larger body size, wider gapes, and higher bite forces (Perez-Mellado and de la Riva 1993; Herrel et al. 1996, 1999*b*; Santos et al. 2000), or lead only to an increase of the dietary spectrum in larger individuals.

While the role of sexual and natural selection in shaping variation in maximal bite force across individuals has been studied previously (Verwaijen et al. 2002; Husak et al. 2006; Lailvaux and Irschick 2007; Herrel et al. 2010), bite duration has never been thoroughly investigated, despite its potential importance for both social and ecological tasks. How long individuals can sustain their bite and how this interacts with maximal biting capacity are relevant for antagonistic contests, where males frequently "head lock" in fighting position, biting the head of their opponents for prolonged intervals, producing injuries (Lailvaux et al. 2004; Lappin and Husak 2005) and increased predation risk (Cooper and Vitt 2002). The same is the case during mating: in several lizard species, males bite the females to immobilize them and copulate with them (Galán 1997). Therefore, it is reasonable to predict that sexual selection may act to enhance biting endurance, where males able to sustain their bites for longer would have a reproductive advantage (Olsson et al. 2004). Similarly, biting duration may also be under the influence of natural selection and potentially contribute to resource segregation both across individuals in general and among specific age and sex groups (e.g., males being able to consume larger or harder prey than females or resulting in ontogenetic variations in diet) through its influence on prey manipulation. Despite its strong potential for being a sexual and a natural selection agent, bite duration has never been examined in light of sexual differentiation. Indeed, the proximate determinants of such dimorphism and its relation to other sexually dimorphic traits of the head remain unexplored.

Indeed, the different functions of the head may easily yield conflicting demands and promote the appearance of trade-offs among different performance components. In this sense, maximal bite force and bite duration are traits that may be predicted to trade off for both physiological and biomechanical reasons. First, a trade-off between force and duration can be expected when considering muscle composition. Animals may differ in muscle contractile properties depending on whether biting is optimized for force or for duration. Maximum force will require more fast-twitch muscle fibers—white muscle—capable of producing higher forces but easily exhausted. On the other hand, if an animal needs to optimize duration, it will need slow-twitch muscle fibers—red muscle—not capable of producing such high forces but less easily fatigued (Herrel et al. 1999*a*; Wilson et al. 2002). Second, biomechanical conditions, such as gape angle and biting position, may influence bite force and bite duration (Dumont and Herrel 2003; Anderson et al. 2008; Curtis et al. 2010). Similar to the functioning of a simple lever system, an increase in gape angle decreases bite force (Dumont and Herrel 2003; Curtis et al. 2010), and bite force increases as the point of bite exertion is shifted to the posterior part of the jaw (Dumont and Herrel 2003; Anderson et al. 2008; Curtis et al. 2010). Therefore, the combination of gape angle, biting position, and morphological traits may lead to the optimization for bite force magnitude or duration, depending on the functional demands—antagonistic contests, copulation events, and even prey consumption.

In this study, we take an innovative approach to head functional morphology in order to examine how different functional components of biting performance are optimized for different demands during ecologically and socially relevant tasks. First, we incorporate the examination of a novel trait related to biting, bite duration, allowing us to understand the relationship between this functional trait and head morphology and to investigate whether males and females differ in bite duration, as is the case for bite force. We hypothesize that bite duration will also be sexually dimorphic, as is the case for bite force, where larger head size in males may yield higher performance capabilities. Second, to test how different biting positions (i.e., with respect to gape angle and anteroposterior position, which are known to influence bite force; Dumont and Herrel 2003) may lead to differences in performance across ecological and social tasks, we use four different experimental setups—a combination of two gape angles (narrow vs. wide) and two biting positions (frontal vs. lateral). Because of biomechanical rules, we expect force to be higher when animals bite with the back of the tooth row—lateral position—than when biting frontally (Meyers et al. 2018) and at narrow as compared with wide gape angles (Dumont and Herrel 2003; Meyers et al. 2018). However, how biting duration may respond to these different setups is not easy to predict, as it will depend on its relation with both bite force and morphological traits. Finally, given that optimal functional capacities may require opposing morphological, biomechanical, or physiological adaptations (Stearns 1992), we investigate, for the first time, possible trade-offs between force and bite duration performance and their association with morphological traits. As different morphological configurations may contribute to optimize different functional demands, we test for the existence of many-to-many mapping using the F-matrix approach to relate several phenotypic traits to several performance variables at the intraspecific level (Ghalambor et al. 2003; Walker 2007; Bergmann and McElroy 2014).

Material and Methods

To investigate sexual dimorphism in bite duration, its relation to morphology, and the possible existence of trade-offs with bite force, we focused on the wall lizard *Podarcis bocagei*, a lacertid endemic to the northwestern Iberian Peninsula. This species is highly dimorphic in body size, relative head size, and head shape (e.g., Kaliontzopoulou et al. 2010). Lizards for this study were captured in a single population from northern coastal Portugal in the coastal dunes of Madalena (41.10°N, 8.66°W). We selected a coastal dune population because it exhibits more marked sexual dimorphism than those from other habitats (Kaliontzopoulou et al. 2010). We collected a total of 43 adult individuals, including 17 females and 26 males, by noose (García-Muñoz and Sillero 2010) in April 2016. Lizards were placed in cloth bags, transported to the laboratory, and housed in individual terraria, where they were fed live mealworms and provided water ad lib.

For all individuals captured, we measured snout-vent length (SVL), head length (HL), head width (HW), head height (HH), and lower jaw length (LJL) using electronic calipers (precision: ± 0.01 mm). These head traits were selected because they are the main morphological determinants of bite force (e.g., Herrel et al. 2001*b*; Kaliontzopoulou et al. 2012). Bite force was measured using an isometric Kistler force transducer (type 9203, Kistler, Winterthur, Switzerland) mounted on a vertical holder and connected to a Kistler charge amplifier (type 5058A). Bite force measurements were obtained by provoking the lizard to bite a pair of thin metal plates connected to the force transducer (see Herrel et al. 2001*b* for a detailed description). Bite performance was recorded and viewed on a laptop using the DATAQ Instruments DI-149 data acquisition device and WinDaq Waveform Browser software (DATAQ Instruments, Akron, OH). The tip of the metal plates where the lizard bit was delimited with a marker to ensure all lizards bit at an equal distance from the fulcrum and thus standardize the point of force exertion. The tip was padded with insulating tape to provide grip and avoid damage to the teeth.

We examined two gape angles—narrow and wide—and two bite positions—frontal and lateral—which resulted in four experimental setups: narrow frontal (NF), narrow lateral (NL), wide frontal (WF), and wide lateral (WL). These conditions were designed before the beginning of the experiments for data collection to simulate biomechanical alternatives within the range of gape aperture allowed by the morphological properties of the species. This resulted in a mean angle of approximately 33° for the narrow and approximately 42° for the wide biting settings. Because of gape constraints, females performed only in the narrow gape angle experiments. Importantly, these settings were chosen to simulate functionally and ecologically relevant situations. Frontal biting is typically used in social interactions, where during mating males sustain their biting of the flanks of females at narrow gape angles, while male antagonistic encounters involve wide gape biting of the opponent for variable time intervals. On the other hand, frontal, narrow gape, fast biting is possibly more relevant for prey capture, but lateral biting is also known to be used for prey manipulation, particularly when dealing with long and hard prey items. Each lizard was tested five times in each setup to ensure that the maximal bite force per individual was registered and retained for further analyses. We allowed a rest of at least 30 min between trials to ensure physical recovery of the individuals. Bite duration was then obtained using the maximal bite force curve profile (e.g., Herrel et al. 2001*b*) recorded for each individual. To obtain bite duration, the onset and offset of biting were determined by the time at which the bite force curve crossed 50% of its maximal value.

Statistical Analyses

All morphological and bite performance variables were log transformed before analyses. To represent total head size (HS), we used Mosimann's (1970) geometric mean approach and calculated HS as the third root of the product of the logarithms of HL, HW, and HH.

We first investigated sexual dimorphism in bite performance using multivariate ANOVA (MANOVA) comparisons with each bite performance trait (bite force or bite duration) at different gape angles (narrow vs. wide) separately as the response variable and with sex as the predictor. We also performed the same analysis with HS as a covariate. We used permutation-based MANOVA with 1,000 randomizations of Euclidean distance matrices, as implemented in the adonis function of the vegan R package (Oksanen et al. 2017). Because bite duration has never been investigated before, we also performed multivariate ANCOVA comparisons with each bite duration at different bite positions (frontal and lateral) separately as the response variable, each head dimension and sex as predictors, and HS as a covariate to explore size-free dependence of bite duration on head morphology. To investigate how the biting setup influenced biting performance, we performed repeated-

Table 1: Results of ANOVA comparisons performed separately on each type of biting performance with sex as a predictor (model 1) and including HS as a covariate (model 2)

	Model 1		Model 2			
	Sex		HS		Sex	
	F	*P*	*F*	*P*	*F*	*P*
Maximum force NF	246.330	**.001**	704.03	**.001**	7.09	**.018**
Maximum force NL	198.480	**.001**	360.86	**.001**	5.59	**.019**
Duration NF	.607	.369	1.185	.28	.307	.586
Duration NL	5.383	**.019**	5.766	**.023**	.067	.771

Note. Significant effects are indicated with boldface type. See "Material and Methods" for variable abbreviations. Total degrees of freedom are 41 in all comparisons.

measures ANOVA on maximum bite force and bite duration of each sex separately, with the experimental setup as a fixed factor and individual as a random factor.

To test for a trade-off between raw force and duration of biting among individuals, we examined the fit of a general linear mixed model with bite duration (NF) as the response variable, bite force (NF) as a fixed predictor, and individual as a random effect. In this case, we used all five biting measurements registered for each individual instead of the maximal curve alone because data encompassing within-individual variation are more robust for testing for the occurrence of performance trade-offs (Roche et al. 2016; Careau and Wilson 2017; Lailvaux et al. 2019). We used the NF setup for this test because this is the experimental setup most commonly used for measuring variation in bite force in the literature (Herrel et al. 2001*b*). Mixed effect models were fit using the lme4 R package (Bates et al. 2015), and corresponding ANOVA statistics were calculated using the car R package (Fox and Weisberg 2011).

To understand the relationship between morphology and function and to investigate many-to-many mapping (sensu Bergmann and McElroy 2014), we used F-matrix statistics to explore the association between head dimensions and biting performance and to test for possible morphological trade-offs between force and duration. This method allows us to disentangle the complex relationship between phenotypic traits and several performance variables. By interpreting the values in the F-matrix we can infer (1) trade-off relationships, where an inverse relationship exists between two performance measures, leading to a conflicting functional demand on a phenotypic trait; (2) facilitation, where similar functional demands are imposed on a phenotypic trait (i.e., the inverse of trade-off); and (3) one-to-one relationships, where a performance trait is influenced by a single phenotypic trait only.

SVL and head linear measurements were used as phenotype variables, and the two recorded bite functional traits were used as performance variables. To obtain the intraspecific F-matrix, we used the fmat function for R (Bergmann and McElroy 2014). We performed this analysis with both sexes together and for each sex separately. Because morphology-function relationships may differ between the sexes because of other factors (e.g., muscle physiology, behavior, etc.), we then used a Mantel test of matrix association with 1,000 randomizations (as implemented by Bergmann and McElroy 2014) to compare the male versus female F-matrices. In the case of males, we also performed a more integrative analysis with performance measurements for all four experimental setups. Throughout, we used effect sizes to determine which values to consider interpretable, considering effects of 0.3–0.5 as "medium" and effects >0.5 as "large" (Cohen 1988). All statistical analyses were performed using R version 3.4.3 (R Development Core Team 2017).

Results

ANOVA comparisons revealed significant differences between the sexes in maximum bite force for narrow gape with different bite positions (NF and NL), where males attained a higher maximal bite force than females (table 1; fig. 1), and these differences remained significant after accounting for variation in HS (table 1). Significant differences also existed in the

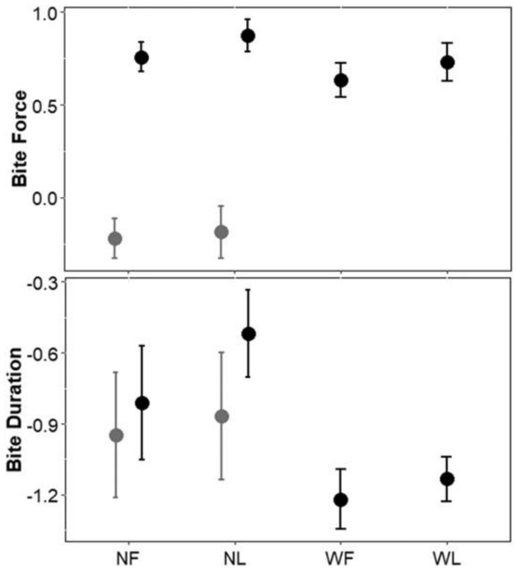

Figure 1. Least squares means observed in males (black) and females (gray) for maximum bite force (*top*) and bite duration (*bottom*). Vertical bars denote 95% confidence intervals. See "Material and Methods" for variable abbreviations.

Table 2: Results of ANCOVAs performed separately on bite duration for frontal and lateral bite positions with different head dimensions (X) and sex as predictors and with HS as a covariate

	HL		HW		HH		LJL	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Duration NF:								
HS	1.145	.275	1.183	.297	1.130	.301	1.277	.279
X	.681	.403	1.786	.184	.178	.682	4.012	**.047**
Sex	.259	.641	.220	.620	.286	.600	.007	.937
X : Sex	.033	.849	.242	.624	.001	.983	1.322	.248
Duration NL:								
HS	5.760	**.017**	5.822	**.019**	6.250	**.015**	5.538	**.027**
X	1.124	.293	1.035	.301	4.503	**.041**	.301	.587
Sex	.045	.839	.106	.741	.092	.760	.209	.654
X : Sex	.860	.365	1.305	.262	.750	.390	.014	.926

Note. Significant effects are indicated with boldface type. See “Material and Methods” for variable abbreviations. Total degrees of freedom are 41 in all comparisons.

duration of bite performance for NL bites, where males sustained their bites longer than females (table 1; fig. 1). However, this effect was rendered nonsignificant after accounting for HS effects (table 1). ANCOVA tests in the frontal biting setup indicated that only LJL had a significant effect on bite duration after size effects were taken into account (table 2). In the case of lateral biting, only HH had a significant effect (table 2). Repeated-measures ANOVA indicated that males attained higher bite forces when biting at the back of the tooth row—lateral position—compared with biting at the front, and this was the case at both gape angles examined (table 3; fig. 1). Bite duration at a narrow gape angle was significantly higher during lateral biting compared with frontal biting in males (table 3; fig. 1). In the case of females, we did not detect significant differences between the different setups (table 3; fig. 1).

The linear mixed effects model used to investigate the trade-off between raw values of bite duration and bite force (NF setup) while taking within-individual variation into account was not significant ($F = 0.31$, $P = 0.58$).

The examination of F-matrix statistics considering both sexes together (table 4) revealed that HL is involved in one-to-one relationships, where animals with longer heads exhibit higher durations at narrow gapes and frontal bite position. By contrast, HH was involved in facilitation, where higher heads were associated with higher bite forces and longer durations in both narrow and frontal bites. Moreover, we detected a trade-off that involved LJL, where longer lower jaws increased bite force but decreased duration in narrow and frontal bites. When analyzing males and females separately, we identified one-to-one facilitation and trade-off relationships that varied between the sexes (see table S1, available online). However, the comparison of the two F-matrices did not identify significant differences (Mantel $r = 0.109$, $P = 0.612$), and as such, we renounced further interpretation of sex-specific matrices and focused on the pooled-sexes analysis (table 4). When examining the extended data set including all four biting setups available for males, we detected additional trade-offs and facilitations (table 5). Three morphological variables were involved in trade-offs of biting performance: (1) higher SVLs were associated with longer bites in NL but shorter bites in WF and decreased bite forces in WL; (2) longer heads increased biting duration in NF, WF, and WL but decreased bite force in WL; and finally, (3) longer lower jaws caused higher bite forces in all experimental setups but a decrease in duration in three of the four setups (NF, WF, and WL). Moreover, HH was again involved in facilitation, where higher heads were associated with higher bite forces in NF, WF, and WL and also with higher biting duration in NL.

Discussion

Our investigation of the different functional components of bite performance revealed that trade-offs, facilitation, and one-to-one relationships are simultaneously involved in the morphological optimization of bite force and bite duration (tables 4, 5, S1). The examination of this novel functional trait, never previously considered, and the integration of our results through the recently proposed F-matrix approach shed new

Table 3: Results of repeated-measures ANOVAs performed between different types of biting performance in each sex separately

	Males		Females	
	F	*P*	*F*	*P*
Maximum force:				
NF vs. NL	7.766	**.010**	2.453	.137
WF vs. WL	19.630	**1.77×10^{-4}**	. . .	. . .
Duration:				
NF vs. NL	6.752	**.016**	.321	.579
WF vs. WL	1.826	.189	. . .	. . .

Note. Significant effects are indicated with boldface type. See “Material and Methods” for variable abbreviations. Total degrees of freedom are 24 for males and 16 for females in all comparisons.

Table 4: F-matrix for both sexes of *Podarcis bocagei* showing standardized partial multiple regression coefficients

	NF	Duration NF	NL	Duration NL	Sum	Variance
SVL	−.018	−.214	−.029	−.221	−.481	.013
HL	.118	**.862**	.151	−.083	1.049	.171
HW	.177	−.105	.070	−.227	−.086	.032
HH	*.311*	**.569**	.115	**.971**	1.966	.137
LJL	*.413*	**−1.005**	**.668**	−.143	−.067	.549
Sum	1.036	2.756	1.034	1.646	6.471/3.65	
Variance	.024	.154	.069	.132		

Note. Row sums and variances, column sums and variances of the absolute values, and grand sums of absolute values for columns (before slash) and rows (after slash) are shown. Values of medium and large effect size are indicated by italic (0.3–0.5) and boldface (>0.5) type, respectively. See "Material and Methods" for variable abbreviations.

light on the evolution of biting functional morphology in lizards, suggesting that opposing selective pressures acting on bite performance underlie variation in some morphological traits, which cause bite force to increase at the cost of a reduction in bite duration or the other way around. In terms of the selective forces driving this functional system, maximal bite force seems to be under stronger sexual selection than duration: while our results reinforce the well-established pattern of higher bite forces in males, both during frontal and posterior biting, we did not identify remarkable differences between the sexes in terms of bite duration (but see below). The comparison of within-sex variation of experimental setups sheds more light on the possible causes of bite performance variation, where only male performance varies across different tasks, a fact that suggests an important role of mainly social behaviors but also with potential consequences for ecological functions.

Indeed, complementing previous knowledge on the biting functional system, we found that, contrary to the marked sexual differentiation observed for bite force, bite duration was similar between the sexes (table 1). While males attained higher bite forces than females even when correcting for HS, a pattern typical of many lizard species (e.g., Herrel et al. 1999*b*, 2001*b*; Husak et al. 2006; Kaliontzopoulou et al. 2012), bite duration was significantly different between the sexes only in the NL setup, and this difference was mainly driven by HS. Indeed, bite duration is possibly more related to muscle architecture (presence/absence and position), which is known to exhibit few differences between males and females of other *Podarcis* species, although total adductor mass is much higher in males (Herrel et al. 1996). Therefore, while muscle characteristics that are more associated with biting endurance, such as the type and position of muscles, do not seem to be different between the sexes, the increase in total adductor muscle mass in males can presumably result in a higher bite force (Herrel et al. 2001*a*), as we observed in our data. It is worth noting that this combination of similar biting duration between the sexes with higher maximal bite force in males could still result in sexual differences both in the array of potential prey and in exposure to predators. Because biting duration as measured here corresponds to 50% of the time that the maximal bite force is sustained, males are able to apply much higher bite forces in the same time interval, which is likely to enhance their efficiency for immobilizing prey, minimizing manipulation, and hence reducing exposure to predators (Edwards et al. 2013).

To shed more light on the determinants of bite performance and what might be causing sexual variation in this functional system, we examined how the magnitude and duration of biting potentially vary when different social and ecological behaviors are simulated through different experimental configurations. We found that bite performance varies only in males (table 3), which provides evidence for a previously unexplored functional differentiation between the sexes, suggesting an important role

Table 5: F-matrix for males of *Podarcis bocagei*, considering all four experimental setups, showing standardized partial multiple regression coefficients

	NF	Duration NF	NL	Duration NL	WF	Duration WF	WL	Duration WL	Sum	Variance
SVL	.245	−.165	.002	**−.815**	.288	*.320*	*.391*	−.141	.125	.158
HL	−.138	**.780**	−.194	.197	−.171	*.457*	*−.432*	*.423*	.923	.171
HW	.140	.031	.243	.254	.262	−.126	.012	−.164	.652	.029
HH	*.361*	.080	−.074	**.501**	*.300*	.096	*.438*	.246	1.948	.039
LJL	*.338*	**−.757**	**.731**	.225	*.321*	**−1.013**	**.551**	*−.419*	−.013	.409
Sum	1.222	1.802	1.243	1.993	1.341	2.011	1.824	1.394	12.832/3.660	
Variance	.011	.138	.082	.069	.003	.138	.042	.018		

Note. Row sums and variances, column sums and variances of the absolute values, and grand sums of absolute values for columns (before slash) and rows (after slash) are shown. Values of medium and large effect size are indicated by italic (0.3–0.5) and boldface (>0.5) type, respectively. See "Material and Methods" for variable abbreviations.

for social pressures but also bearing potential ecological implications. The role of bite force in both social and ecological tasks is well understood in lizards: higher bite force allows males to have larger territories (Lappin and Husak 2005), win fights (Lailvaux et al. 2004; Huyghe et al. 2005), have access to more females (Lappin and Husak 2005), and consume larger and harder prey (Stamps 1977; Preest 1994; Herrel et al. 1999*b*). However, the innovative approach of comparing bite performance across ecological and social tasks taken here sheds new light on the fine-tuning of sexual differentiation in this functional system. Indeed, we found that males have higher bite performance—both force and duration—when biting with a narrow gape than with a wide gape (table 3; fig. 1). Similarly, the results obtained through the comparison of frontal versus posterior biting suggest that males—but not females—may further enhance their already higher bite forces when biting at the posterior region of their tooth row. This kind of behavior is displayed during prey manipulation when consuming long and hard prey (Herrel et al. 1999*b*; Meyers et al. 2018), and our results suggest that increased posterior biting performance in only one sex could contribute to the differences in the prey size spectrum between sexes, as males may use this tactic to gain access to larger and/or harder prey (Herrel et al. 1999*b*; Meyers et al. 2018). From a previous study, we have little evidence of strong dietary divergence between sexes in *Podarcis bocagei*, but males consumed relatively harder prey than females (Kaliontzopoulou et al. 2012), possibly as a result of the higher biting capacity of males when using the posterior part of their jaw, documented for the first time in this study.

According to mating behavior, it is reasonable to predict that bite duration may be differentially important in both sexes, potentially yielding sexual differences in this trait. Males of *P. bocagei* bite females in the flanks during copulation, which can last from 22 to 30 min (Galán 1997), a behavior known to occur in several other lizard species (e.g., *Algyroides* sp., *Iberolacerta* sp., *Lacerta* sp., *Timon* sp., and *Zootoca* sp. in Arnold et al. 2007). This type of social pressure on biting performance was simulated here through the NF experimental setting, as males hold females by biting them with a relatively small gape and in a frontal position. However, our results do not support the prediction that sexual selection related to mating behavior may drive sexual dimorphism in bite duration, as males and females did not differ in bite duration in NF (table 1). Nevertheless, these results need to be taken with some caution, as they might be due to methodological or even behavioral aspects. First, bite duration, as measured here, may not directly reflect this behavior. In our study, we used the bite force curve to extract bite duration, and we obtained the time at which the bite force curve crossed 50% of its maximal value. However, during copulation, males are not expected to perform at their highest force capacity, as this could cause serious injuries to females, a strategy that would not be evolutionarily favorable. To definitely evaluate the relevance of biting endurance for male reproductive fitness, one would need to uncouple maximal bite force from the capacity to sustain the bite, which would be particularly difficult to simulate under laboratory conditions. Furthermore, bite performance used in fighting behavior between males was simulated here with the wide gape setup, where males with high bite forces are expected to win more combats. Because males have bigger heads than females, they performed at wide gapes, but performance decreased in both force and duration compared with bite performance at narrow gapes. Bite performance is important in antagonistic interactions, but our results suggest that this behavior is not the most important selective force on bite performance. Despite these new insights into the specific tasks contributing to variation in bite performance, only the investigation of male antagonistic encounters in laboratory conditions could definitely answer whether not only bite force (Huyghe et al. 2005; Abalos et al. 2016) but also bite duration may predict the outcome of combats.

Theoretically and according to the behavior of this and other lizard species, all the aforementioned social and ecological tasks would benefit if bite force and bite duration could be optimized at the same time. The integration of the results obtained for the two biting performance traits and their variation across ecological and social tasks with morphological variation using the F-matrix approach suggests that HH is a facilitation trait that contributes to such optimization, as it increases both bite force and bite duration (in both sexes or in males separately). This adds to previous knowledge about the role of HH in driving bite performance and extends our understanding of why this trait is one of the main dimorphic characters in many lizard species (e.g., Herrel et al. 2001*a*; Husak et al. 2006; Kaliontzopoulou et al. 2012). Indeed, it seems that the augmentation of internal muscle mass enhanced through an increase of HH (e.g., Herrel et al. 2001*a*, 2001*b*; Thomas et al. 2015) not only contributes to higher bite forces but also amplifies the capacity to sustain a bite for longer intervals. Since maximum HH was measured at the posterior, higher region of the head, as is typically done in lizard biometrics, we can hypothesize that this may be the result of increased space for jaw adductor muscles. Yet this remains to be investigated using morphology and physiology of the head muscles in males and females of *P. bocagei*.

Despite this pattern of morphological facilitation of functional performance, the production and maintenance of phenotypic traits may depend on evolutionary and biomechanical constraints, as well as on physical space and correlations with other traits (e.g., muscle physiology; Irschick and Higham 2016). As such, optimization of one trait usually occurs at the cost of another because of mechanical or physiological trade-offs (Lailvaux and Husak 2014; Irschick and Higham 2016). Our results support this idea, as we found that trade-offs occurred at a much higher frequency in the biting functional system of *P. bocagei* compared with the single aforementioned case of facilitation. Indeed, while a trade-off between bite force and bite duration was not evident when examining raw traits, an evolutionary trade-off was clearly suggested through the analysis of morphology-function relationships. Our results indicate that an increase in LJL leads to an increase in bite force but a decrease in bite duration (table 4). We also found that—when analyzing males separately—an increase in HL was associated with an increase in bite duration and a decrease in bite force, supporting the same reasoning for a morphological trade-off. A trade-off between force and duration can be expected, taking into account head morphology and associated muscle physiology. Animals with longer lower jaws will have more space in the posterior part of the jaw where the external adductors of the jaw attach (i.e., the musculus adductor mandibulae externus superficialis, MAMES). This muscle is composed of more fast fibers that could then insert onto the lateral side of the lower jaw and/or increase pennate muscle (Herrel et al. 1996, 1999*a*), potentially explaining the observed increase in bite force. On the other side, the increase of bite duration in males associated with longer heads (in total) may be associated with an increase of the musculus pterygoideus (MPt), which is composed of slower fibers (Herrel et al. 1996, 1999*a*). The use of specific muscles for certain performance traits (LJL [MAMES] for bite force, HL [MPt] for bite duration) and/or with different physiology (LJL [fast fibers] for bite force, HL [slow fibers] for bite duration) can lie at the origin of the trade-off detected in our data. However, these hypotheses are largely based on studies of muscle physiology in other phylogenetically distant lizard species (i.e., lizards of the genus *Uromastix* and *Plocederma stellio*; Herrel et al. 1999*a*), and as such, a comprehensive investigation of the physiology of head muscles in *P. bocagei* would be necessary to test them.

In summary, we detected small sexual differences in bite duration, suggesting that this component may be less important than maximal bite force in the context of sexual selection. However, the integration of this novel performance trait and the use of different experimental setups allowed us to detect possible causes of bite performance variation, demonstrating the importance of bite performance in ecological tasks and in social behavior in males. Remarkably, our results also suggest the existence of trade-offs in the morphological optimization of maximal capacity and bite duration, possibly due to physiological constraints on muscle composition, insertion, and orientation. This study revealed the importance of incorporating multiple variables in a more integrative analysis of bite performance, and it is a first important step toward understanding biting and the selective pressures driving its evolution in lizards and other organisms. Future work is needed to help us understand the relationship between internal morphology and bite performance and to include not only bite force and duration but also bite endurance, which will allow us to establish links with mating behavior and potentially with fitness. Furthermore, it would be relevant to investigate whether the trade-offs identified here are also observed in other species, populations, or animals using other habitat types, as all these factors are known to influence social and ecological behavior.

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