



Relationships between dietary breadth and flexibility in jaw movement: A case study of two recently diverged insular populations of *Podarcis* lizards

Maxime Taverne^{a,*}, Thierry Decamps^a, Oscar Mira^b, Iva Sabolić^b, Joao Duarte Da Silva^a, Marko Glogoški^b, Duje Lisičić^b, Anamaria Štambuk^b, Anthony Herrel^a

^a Département Adaptations du Vivant, Muséum national d'Histoire naturelle, Centre National pour la Recherche Scientifique, Paris, France

^b Faculty of Science, Department of Biology, University of Zagreb, Croatia

ARTICLE INFO

Editor: Michael Hedrick

Keywords:

Dietary generalist
Dietary specialist
Jaw kinematics
Prey type
Stereotyped movements

ABSTRACT

The kinematics of lizard feeding are the result of complex interactions between the craniocervical, the hyolingual, and the locomotor systems. The coordinated movement of these elements is driven by sensory feedback from the tongue and jaws during intraoral transport. The kinematics of jaw movements have been suggested to be correlated with the functional characteristics of the prey consumed, such as prey mobility and hardness. However, whether and how dietary breadth correlates with the flexibility in the behavioral response has rarely been tested, especially at the intraspecific level. Here we tested whether an increase in dietary breadth was associated with a greater behavioral flexibility by comparing two recently diverged populations of insular *Podarcis* lizards differing in dietary breadth. To do so, we used a stereoscopic high-speed camera set-up to analyze the jaw kinematics while offering them different prey types. Our results show that prey type impacts kinematics, especially maximum gape, and maximum opening and closing speed. Furthermore, the behavioral flexibility was greater in the population with the greater dietary breadth, suggesting that populations which naturally encounter and feed on more diverse prey items show a greater ability to modulate their movements to deal with variation in functionally relevant prey properties. Finally, the more generalist population showed more stereotyped movements suggesting a finer motor control.

1. Introduction

Resource use in depauperate environments can be challenging. In insular populations of lizards, where food is typically scarce and intra-specific competition is often high (Pafilis et al., 2009; Itescu et al., 2017), dietary shifts towards generally unexploited resources are frequently observed (Van Damme, 1999; Bolnick, 2001; Herrel et al., 2008). Dietary changes in insular populations are often accompanied with anatomical specializations compared to their mainland counterparts (Schoener, 1977; Perry, 1996; Thomas et al., 2009). However, alterations in ecological dynamics are likely to impose selection primarily on performance and behavior rather than on anatomy (Arnold, 1983; Irschick et al., 2008). Because foraging and feeding are undoubtedly among the most critical aspects of an organism's daily activities, how these traits vary along with environmental fluctuation has been widely investigated (see Schwenk, 2000; Reilly et al., 2007 for an overview).

Behavior associated with resource use is typically quantified by

focusing on jaw and tongue kinematics, which allows inference of the link between anatomy, bite force, and diet (Herrel et al., 1998; Meyers et al., 2002; Curtis et al., 2009; Herrel and De Vree, 2009). Feeding consists of four major components: prey location, capture, intraoral transport, and swallowing. These tasks are assured by the interplay between the craniocervical, the hyolingual, and the locomotor systems (Montuelle et al., 2009; Montuelle et al., 2012). All those systems have to work together, and still each is differentially involved depending on the step of resource acquisition and on the taxon considered. For example, the tongue is used to capture prey in some taxa (see in Chameleontidae: Wainwright and Bennett, 1992); Agamidae: Schwenk and Throckmorton, 1989; Kraklau, 1991; Iguanidae: Schwenk and Throckmorton, 1989, Bels, 1990; Scincidae: Smith et al., 1999; Cordylidae: Broeckhoven and Mouton, 2013) and plays an important role in intraoral transport and swallowing in most lizards. The role of the tongue has drawn more attention since it has been suggested to provide sensory feedback during intraoral transport, especially during the

* Corresponding author.

E-mail address: maxime.taverne@aphp.fr (M. Taverne).

<https://doi.org/10.1016/j.cbpa.2021.111140>

Received 30 November 2021; Received in revised form 28 December 2021; Accepted 28 December 2021

Available online 31 December 2021

1095-6433/© 2021 Elsevier Inc. All rights reserved.

slow-opening phase (Herrel et al., 2001; Schaerlaeken et al., 2008).

Lizards are able to modulate their tongue and jaw kinematics in response to prey characteristics, including prey type (Herrel et al., 1996a; Schaerlaeken et al., 2011), hardness (Herrel et al., 1999b; Metzger, 2009), mobility (Schaerlaeken et al., 2008; Montuelle et al., 2010), and size (Montuelle et al., 2009; Broeckhoven and Mouton, 2013). It is often assumed that the flexibility of the behavioral repertoire and the diversity of the prey included in the diet are correlated, yet this remains rarely tested. Hence, animals which encounter a wide variety of prey in their environment (generalists) are thought to be more likely able to modulate their behavioral response than specialists (e.g. in fishes, see Liem, 1978; Van Wassenbergh et al., 2006; in lizards: Herrel et al., 1999a, 1999b).

Despite the relatively thorough understanding of the factors driving variability in feeding behavior and kinematics, they have rarely been investigated at the intraspecific level. Nevertheless, diet can be highly variable among populations of the same species, especially in insular systems (Schoener, 1977; Brown and Perez-Mellado, 1994; Sagonas et al., 2014; Donihue et al., 2016; Taverne et al., 2019). How intraspecific variability in diet might affect the behavioral response remains unknown to date. Here, we test how a change in diet affects the jaw kinematics and kinematic flexibility in two recently diverged populations of *Podarcis siculus* (Rafinesque Schmalz, 1810). Whereas one of these populations is insectivorous, the other includes a large proportion of plants into its diet (over 60%) and shows an increased dietary breadth.

The aim of this study was to test whether the increased dietary breadth observed in the omnivorous population is associated with an increase in the flexibility (sensu Wainwright et al., 2008) in jaw kinematics when feeding on insect prey differing in their properties and size. Moreover, we explored whether males and females differ in the kinematics of intraoral transport given their difference in head morphology, bite force, and diet (Herrel et al., 2008; Taverne et al., 2019; Taverne et al., 2020). We specifically predict that: 1) the type of prey should impact the jaw kinematics, 2) males and females should respond differently to changes in prey type with males showing lower absolute gape angles and shorter cycle times given their relatively larger heads and bite forces, 3) the generalist omnivorous lizards from Pod Mrčaru should show a greater flexibility in their feeding behavior compared to the insectivorous and more specialized lizards from Pod Kopašte.

2. Material & methods

2.1. Specimens

Adult specimens from the islets of Pod Kopašte and Pod Mrčaru were captured during the summer 2018 and maintained in captivity in the Zagreb Zoo until the end of winter 2019. Size, body mass and head dimensions of the specimens are detailed in the Table 1. Individuals from both populations were fed with crickets and maintained on a 12 h light / dark cycle. Upon emergence from hibernation animals were moved to the animal care facility of the Museum of natural History in Paris. In total, six individuals were included in the present study: one female and three males from Pod Kopašte and one female and one male from Pod

Mrčaru. The lizards were not fed one week prior to filming.

2.2. Experimental set-up

Each lizard was introduced in a wooden box with an enclosed Plexiglas corridor (Fig. 1). A prey was fixed at the end of the corridor to standardize the position of the prey relative to the lizard while feeding. Each individual was proposed two types of prey (crickets and mealworms), the size of which was adjusted to the size of the individual. We attempted to record, when possible, three trials per type of prey per lizard. Two high-speed Phantom Miro R311 cameras with a 50 mm focal length lens were used to record the feeding bouts. Both cameras were positioned at an acute angle and in a different plane to facilitate the three-dimensional tracking of the jaw tips (Theriault et al., 2014). The two cameras were synchronized and were set to a recording rate of 250 Hz. We ensured that each trial included at least five intraoral transport cycles.

2.3. Calibration of the cameras

The cameras were calibrated using a structure-from-motion approach with sparse bundle adjustment optimization. To do so a 22.5 mm wand was moved through the recording volume. The resulting 3D calibration was rotated such that the +X axis pointed along the length of the chamber, +Y along the width and +Z along the height. The average reprojection error (the difference between fitted and observed wand end point locations) was 0.175 pixels, and the average variation in the 3D length of the calibration wand was 0.7% indicating a high-quality camera calibration. Calibration point locations were collected using DLTdv8 Release 8.1.7 (Hedrick, 2008) and the structure-from-motion calibration was performed using easyWand (Theriault et al., 2014).

2.4. Digitation of the videos

Jaw movements were tracked manually using DLTdv8. Three points were tracked: the tip of the mandible, the tip of the snout, and the *anguli oris* or mouth corner. Each video thus provided over time the (u,v) coordinates of each point, which were ensured to be visible on each view by the relative position of the cameras. Thanks to the DLT coefficient obtained by the calibration procedure, the (u,v) coordinates extracted from the two views were compiled into three dimensional (x,y,z) coordinates that were subsequently used in the analyses. The gape angle and the distance between the tips of the jaw were calculated from these coordinates. The gape angle and distance curves were smoothed using the function "smooth.spline" of the package "stats" in R (R Core Team, 2021). The new angle and distance values generated by the curve smoothing were used to calculate the following 13 variables. We calculated the maximum distance between the tips of the jaw (in millimeters), the maximum gape angle (in degrees), the maximum opening speed, the maximum closing speed (in mm.s⁻¹), the duration of the biting cycle (in seconds), and the absolute and the relative durations of each of the four phases of the jaw cycle (Bramble and Wake, 2013): the slow opening (SO), the fast opening (FO), the fast closing (FC) and the slow closing (SC) (Fig. 2). Each of these variables was obtained for each

Table 1

Body metrics of the specimens included in the present study. f: female, m: male. Body mass is in grams, and all lengths are in millimeters. hl: head length, hw: head width, hh: head height, ljl: low-jaw length, qt: quadrate to tip length, ct: coronoid to tip length.

	Sex	Individual	Body mass	svl	hl	hw	hh	ljl	qt	ct
Pod Kopašte	f	0154	4.7	62.02	13.01	7.43	5.8	13.66	12.49	9.62
	m	0186	6.2	68.21	15.39	9.04	7.28	16.64	15.13	11.21
	m	0148	7.5	65.73	15.8	9.32	8.34	16.71	15.11	11.29
	f	0136	4.6	63.78	13.97	7.91	6.06	14.91	13.43	10.42
Pod Mrčaru	m	0209	7.2	71.23	17.09	9.77	8.37	18.35	16.5	12.47
	m	0165	7.4	72.18	16.67	9.42	7.6	18.04	16.07	12.02
	m	0188	8	68.34	15.48	9.29	7.46	16.88	15.35	11.51



Fig. 1. Picture of the experimental set-up showing the two high-speed cameras pointing to the end of the tunnel where the prey is positioned. Note the relative position of the cameras which are oriented to form an acute angle allowing to optimize camera calibration and to enhance the accuracy of the three-dimensional tracking.

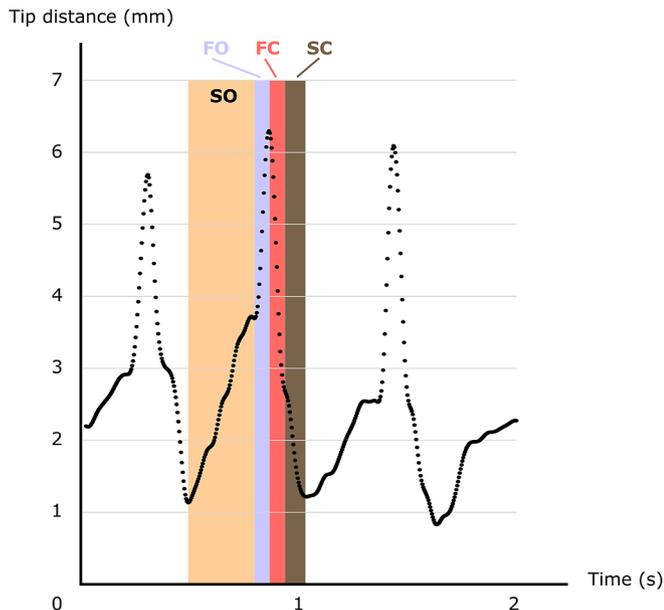


Fig. 2. Smoothed displacement curve illustrating the changes in gape distance over three intraoral transport cycles. Colors illustrate the four kinematic phases of a gape cycle (Bramble and Wake, 2013). Slow opening (SO) generally takes the longest and is associated with the tongue moving under the prey. Next the jaws are opened rapidly during the fast-open phase (FO) allowing the tongue with adhering prey to be retracted in the oral cavity. At maximal gape the fast-closing phase (FC) starts until the jaws hit the prey which determines the onset of the slow-close/power stroke phase (SC) where the prey is crushed.

of the 166 complete cycles recorded (Table 2).

2.5. Statistical analyses

All variables were log₁₀-transformed to assure the normality of the data, except for the relative durations which were arcsin-transformed. To explore the main trends of variability within the dataset and to reduce the number of variables given the small number of observations we performed a factor analysis with varimax rotation and extracted all factors with eigenvalues greater than one. A multivariate analysis of variance (MANOVA) was performed on the axes which cumulatively explained 85% of the variance to investigate the effects of island, sex, prey type, and their interactions on the kinematics of feeding. Subsequent univariate analyses of variances (ANOVAs) were performed on each factor to test which variables drove the observed variation. The feeding repertoire was estimated by calculating the kinematics disparity based on the 13 kinematic variables, using the function “disparity.per.group” (package “dispRity”, Guillerme, 2018). The disparity metrics, which corresponds here to the hypervolume occupied by a group of observations in a multivariate space, was compared between populations, sexes and prey types through Wilcoxon tests including a Bonferroni correction for multiple testing (function “test.dispRity”).

3. Results

The factor analysis extracted five factors which cumulatively explained 93.4% of the variance (Table 3). The first factor was mainly determined by the duration of the phases and of the overall cycle; factor 2 by the maximum gape distance and angle, as well as the maximum opening speed; factor 3 by the absolute and relative durations of the SC phase; factor 4 by the duration of the FC phase; factor 5 by the absolute duration of the FO phase.

The MANOVA showed significant sex and prey effects as well as

Table 2

Mean and standard errors (SE) associated with the tested variables (Dist: maximum gape distance, Angle: maximum gape angle in degrees, Open: maximum opening speed, Close: maximum closing speed, SO/FO/FC/SC: absolute durations of the slow opening / fast opening / fast closing / slow closing phases, r: relative duration, Cycle: duration of a cycle) for each population (PK: Pod Kopašte, PM: Pod Mrčaru), each sex (f: females, m: males), and for each prey type (C: cricket, MW: mealworm). Distances are in millimeters, durations in seconds, and speeds in mm.s⁻¹. The number of cycles considered (Nb) is also indicated.

Island	Sex	Prey	Nb	Dist	Angle	Open	Close	SO	FO	FC	SC	rSO	rFO	rFC	rSC	Cycle	
PK	f	C	18	6.45	32.28	68.00	71.13	0.42	0.08	0.09	0.15	0.56	0.11	0.13	0.21	0.75	Mean
				1.17	5.76	14.58	11.80	0.15	0.02	0.07	0.06	0.10	0.02	0.08	0.09	0.20	SE
		MW	15	5.54	32.30	60.73	82.90	0.36	0.08	0.08	0.11	0.56	0.13	0.13	0.18	0.63	Mean
				0.91	5.26	15.25	15.21	0.12	0.02	0.01	0.07	0.08	0.03	0.03	0.08	0.16	SE
	m	C	23	7.09	31.18	68.96	69.74	0.47	0.08	0.08	0.13	0.60	0.12	0.12	0.17	0.76	Mean
				0.96	4.41	14.49	13.66	0.18	0.01	0.02	0.06	0.11	0.03	0.05	0.07	0.20	SE
		MW	23	5.27	23.69	51.88	67.92	0.44	0.09	0.07	0.15	0.57	0.13	0.10	0.20	0.75	Mean
				1.05	4.94	16.25	27.04	0.16	0.03	0.02	0.07	0.10	0.06	0.03	0.08	0.18	SE
PM	f	C	18	6.90	37.33	72.82	71.55	0.58	0.09	0.09	0.10	0.63	0.12	0.12	0.14	0.86	Mean
				0.65	3.13	13.88	21.60	0.33	0.02	0.03	0.03	0.13	0.04	0.05	0.06	0.36	SE
		MW	12	4.86	24.83	56.96	60.69	0.54	0.08	0.09	0.10	0.65	0.10	0.12	0.13	0.80	Mean
				0.67	3.54	15.99	17.69	0.22	0.02	0.03	0.05	0.14	0.03	0.05	0.08	0.22	SE
	m	C	45	7.87	31.86	75.57	76.95	0.55	0.09	0.08	0.18	0.58	0.11	0.11	0.21	0.89	Mean
				1.31	5.67	17.30	25.74	0.31	0.03	0.03	0.12	0.15	0.04	0.05	0.11	0.37	SE
		MW	12	5.23	21.46	40.89	55.50	0.48	0.09	0.06	0.12	0.62	0.12	0.09	0.17	0.74	Mean
				0.81	3.35	12.42	20.23	0.20	0.03	0.01	0.04	0.10	0.04	0.03	0.06	0.21	SE

Table 3

Results of the factor analysis with VARIMAX rotation carried out on the kinematic variables.

	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
Eigenvalue	3.81	2.67	2.21	1.79	1.66
% variance	29.31	20.50	17.03	13.76	12.80
Max. distance	0.104	0.873	0.147	0.104	0.251
Max. gape angle	0.045	0.891	0.029	0.134	0.248
Max. opening speed	-0.077	0.798	0.001	-0.106	-0.418
Max. closing speed	-0.023	0.647	-0.163	-0.625	-0.137
Duration SO	0.969	0.03	-0.194	0.041	0.124
Duration FO	0.135	0.139	0.091	0.182	0.941
Duration FC	0.046	0.134	0.014	0.949	0.164
Duration SC	0.219	0.032	0.935	0.071	0.114
Rel. duration SO	0.767	-0.037	-0.604	-0.16	-0.114
Rel. duration FO	-0.801	-0.006	-0.063	-0.049	0.563
Rel. duration FC	-0.764	0.022	-0.115	0.601	-0.117
Rel. duration SC	-0.323	0.058	0.924	-0.063	-0.052
Duration of one cycle	0.930	0.087	0.097	0.156	0.245

The variables with loadings greater than 0.7 are indicated in bold.

Table 4

Results of the MANOVA performed on the five first factors testing the effects of island, sex, and prey type on the jaw kinematics.

Effect	Value	F	df hypothesis	df error	P	
Intercept	Wilks'	0.931	2.26	5	153	0.052
Island	Lambda	0.955	1.46	5	153	0.208
	Wilks'					<
Sex	Lambda	0.862	4.92	5	153	0.001
	Wilks'					<
Prey	Lambda	0.553	24.72	5	153	0.001
	Wilks'					<
Island * sex	Lambda	0.951	1.56	5	153	0.174
Island * prey	Wilks'					<
	Lambda	0.888	3.87	5	153	0.002
Sex * prey	Wilks'					<
	Lambda	0.870	4.57	5	153	0.001
Island * sex * prey	Wilks'					<
	Lambda	0.959	1.29	5	153	0.269

The significant results are indicated in bold. F: F-statistic, df: degrees of freedom, P: P-value.

significant interactions between island and prey, and between sex and prey (Table 4). This suggests that the kinematics of feeding differ between prey type and sexes but also that the way individuals of the two populations deal with different prey differs. Finally, males and females also differed in the way they processed mealworms versus crickets.

Specifically, differences between males and females were driven by variation in gape and jaw opening speed with males showing higher gapes and greater speeds than females (Tables 5 and 6).

However, whereas females showed greater gapes and jaw opening speeds when consuming mealworms, males showed higher gapes and opening speeds when eating crickets (Fig. 3). Similarly, whereas individuals from Pod Kopašte used larger gape angles when consuming mealworms, individuals from Pod Mrčaru used larger gapes when consuming crickets (Fig. 3). The kinematic disparity was significantly higher in individuals of Pod Mrčaru (PK: 0.326, PM: 0.368, $P < 0.001$), higher when crickets were consumed (crickets: 0.341, mealworms: 0.291, $P < 0.001$), but did not differ between males and females (females: 0.359, males: 0.334, $P = 0.062$).

Interestingly, no difference in disparity was detected between prey types for individuals from Pod Kopašte (crickets: 0.263, mealworms: 0.236, $P = 0.116$), whereas in Pod Mrčaru, a greater disparity was observed during the consumption of crickets (crickets: 0.299, mealworms: 0.238, $P < 0.001$) (Fig. 4). Furthermore, whereas both populations were equally disparate when eating mealworms ($P = 0.367$), individuals of Pod Mrčaru showed an increase in disparity when eating crickets ($P < 0.001$).

4. Discussion

One of the major drawbacks of the current data set is that only few individuals from each population and sex are included in the study. In particular, because the variability in jaw kinematics of an individual or individuals within species can sometimes be high (Sanderson, 1988), more individuals should be included to conclude on the differences

Table 5

Results of the ANOVAs illustrating the significant effects.

Source	Variable	df	F	P
	Factor 2	1, 157	9.75	0.002
Sex	Factor 3	1, 157	5.11	0.025
Prey	Factor 2	1, 157	104.12	< 0.001
Island * prey	Factor 2	1, 157	17.84	< 0.001
Sex * prey	Factor 2	1, 157	12.18	0.001

F: F-statistic, df: degrees of freedom, P: P-value.

Table 6
Mean ± standard errors (SE) for the variables that differ between the factors tested.

Variable	Island	Sex	Prey	Mean	SE
Factor 2	Pod Kopašte	male	cricket	0.324	0.151
			mealworm	-0.945	0.151
	Pod Kopašte	female	cricket	0.202	0.176
			mealworm	0.006	0.187
	Pod Mrčaru	male	cricket	0.600	0.108
			mealworm	-1.485	0.209
Factor 3	Pod Kopašte	male	cricket	0.632	0.171
			mealworm	-0.817	0.209
	Pod Kopašte	female	cricket	-0.118	0.203
			mealworm	0.202	0.203
	Pod Mrčaru	male	cricket	0.211	0.236
			mealworm	-0.259	0.251
Pod Mrčaru	female	cricket	0.311	0.145	
		mealworm	-0.015	0.281	
Pod Mrčaru	female	cricket	-0.459	0.229	
		mealworm	-0.598	0.281	

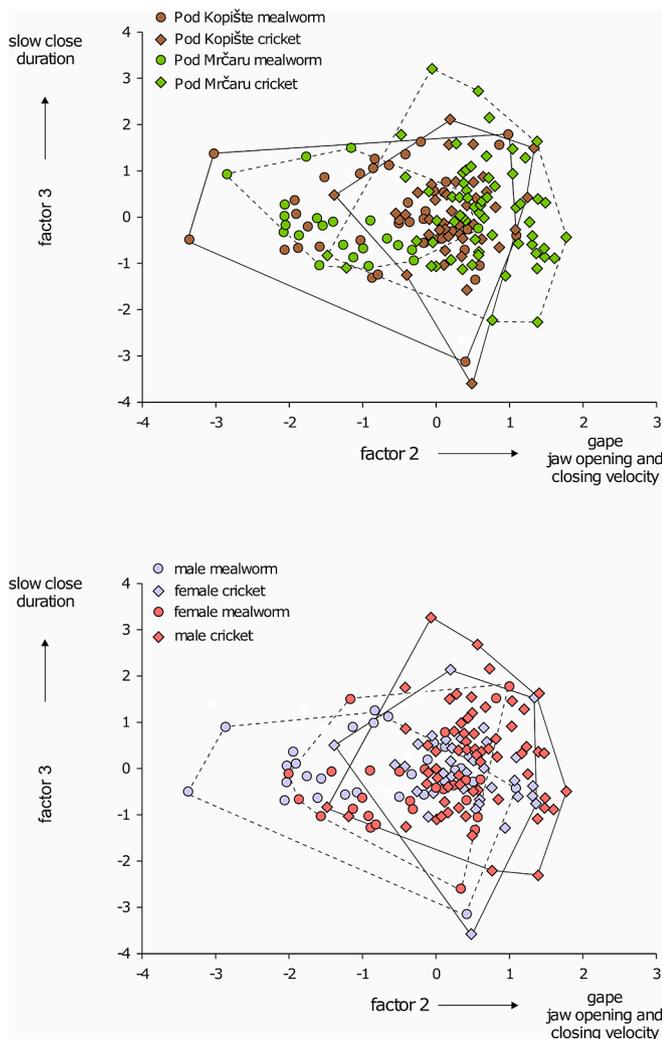


Fig. 3. Plot of the factors two and three showing differences between prey types, populations (top) and sexes (bottom). Circles: mealworms; diamonds: crickets, brown: Pod Kopašte; green: Pod Mrčaru; violet: males; red: females. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

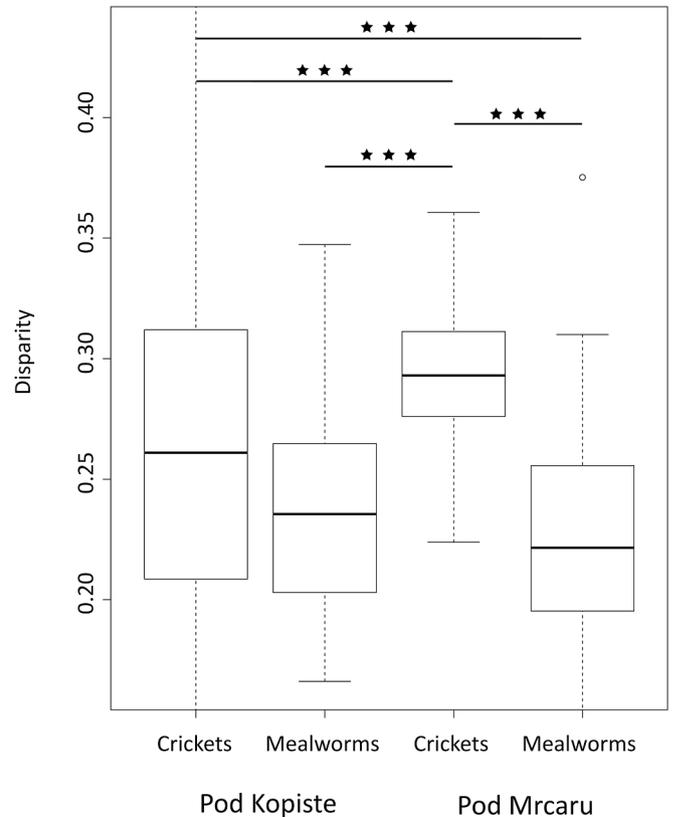


Fig. 4. Plot of the disparity metrics illustrating the differences in kinematic flexibility between the two populations depending on the prey consumed (results of the Wilcoxon's tests for comparison of the means are indicated with three stars, representing a p -value < 0.001). The horizontal traits within the boxes represent the median, the edges of the box represent the first and third quartiles, and the extremities of the whiskers the first and ninth deciles.

between prey types, sexes and populations. Moreover, because the population of Pod Mrčaru naturally includes a great proportion of plant matter in its diet it would be of interest to record the jaw kinematics of the individuals while eating plant matter to better mimic the food items they typically encounter in natural conditions. Although the present results are preliminary and should be interpreted with caution, we believe that they are promising and insightful.

4.1. Effect of prey characteristics

Our results show that prey type is associated with a change in the jaw kinematics, irrespective of the island or the sex. In all cases, the consumption of crickets, which are harder, bigger and more mobile than mealworms, is associated with a greater maximum gape and a maximum opening speed (Fig. 3). The relationship between prey size and maximum gape was also described for *Agama stellio* (Herrel et al., 1996a, 1996b). Intuitively, when eating larger prey, the jaws need to be more widely opened to let the prey move through the oral cavity during intraoral transport. Additionally, the ingestion of more evasive prey is usually thought to be accompanied with a decrease in the duration of the fast opening and closing phases, and with an increase in jaw velocity (Montuelle et al., 2010; Montuelle et al., 2012). This is partly confirmed by our results which demonstrate that individuals increase the maximum opening speed when dealing with the mobile prey (cricket) rather than the slower prey (mealworm). Moreover, on average, feeding disparity increased when consuming crickets compared to mealworms. Our results thus suggest that prey size and evasiveness are important characteristics affecting kinematics as demonstrated previously for other lizards (Schaerlaeken et al., 2008; Metzger, 2009; Montuelle et al.,

2010; Montuelle et al., 2012).

4.2. Effect of sex

As suggested by the ANOVAs, males and females differed in maximum gape distance and angle, the maximum opening speed, and the absolute and relative durations of the slow-closing phase. Whereas the effect of sex on kinematics also depended on the prey, no interaction between sex and island was detected, suggesting that the differences in feeding kinematics between sexes are similar on Pod Kopašte and Pod Mrčaru. Contrary to our prediction, and despite the fact that males are larger than females, males used wider gapes when feeding on crickets. We are not certain why this pattern was observed, but it may be driven by differences in motor control. Studies comparing jaw kinematics between males and females are scarce, and more effort should be undertaken to tackle this question. Additionally, greater bite force was suggested to enable a reduction of prey handling time (Verwajen et al., 2002) by reducing the number of bites necessary to process and swallow prey. Because lizard males usually bite harder than females (Herrel et al., 1996b; Herrel et al., 1999a, 1999b; Kaliontzopoulou et al., 2012; Taverne et al., 2020), we predicted that slow closing phase would be shorter in males, but this was not confirmed by our results. However, in our setup we standardized prey size to the size of the individual. Since prey size and prey hardness are correlated (Verwajen et al., 2002), males were given harder prey than females, which could explain these results. Moreover, there were significant interactions between prey type and sex suggesting that males and females differently treat distinctive prey. For example, whereas males from Pod Kopašte show faster slow close phases for crickets compared to mealworms, in females the slow close phase was shorter for mealworms. Clearly, animals adjust their kinematics in complex ways when confronted with similarly sized prey, which might be associated with the prey they most commonly encounter and eat in the field. Additionally, because males usually use biting for other purposes in natural contexts (e.g., immobilization of the females when copulating, male-male combat, territory defense), the observed differences in jaw kinematics between males and females could be the result of a functional trade-off between the functional role of the jaw system during feeding versus other tasks.

4.3. Behavioral flexibility and stereotypy

The question on whether and how trophic breadth correlates with feeding flexibility has been mostly addressed in fishes (Ralston and Wainwright, 1997; Sanderson, 1988; Sanderson, 1990; Van Wassenbergh et al., 2006; Moran et al., 2018). On the contrary, it has rarely been investigated in tetrapods (but see Herrel et al., 1999b). We predicted that the individuals of the generalist and omnivorous population of Pod Mrčaru will show a greater flexibility in their feeding behavior than individuals of the insectivorous population of Pod Kopašte. Consequently, the disparity in jaw kinematics should be greater in the generalist population. Our results confirmed this prediction, with individuals of the generalist population of Pod Mrčaru increasing their behavioral variability when facing a mobile prey like a cricket. This suggests that the unpredictability of the movements of the prey were overcome by an increased variation in jaw movements and the associated jaw movement speed.

Interestingly, when considering each prey type, the overall variance in the disparity metrics was also lower in the population of Pod Mrčaru (Fig. 4), suggesting that under similar circumstances (i.e. feeding on the same prey type), the generalist lizards did not vary their movement repertoire much. This observation might reveal an increased behavioral stereotypy (sensu Wainwright et al., 2008). A study on the motor pattern in archer fish (Wöhl and Schuster, 2007) suggests that a high flexibility combined with stereotyped movements might reveal a high degree of movement control on the part of the individual. Although the present study does not allow us to draw these conclusions solely based on the

data gathered, our results do suggest that the omnivorous population of Pod Mrčaru might benefit from a finer motor control allowing individuals to modulate their behavioral response when facing different prey types, whilst opting for more stereotyped movements associated with specific prey types.

5. Conclusions

By focusing on the jaw kinematics, the present study investigated how rapid changes in diet between two recently diverged populations impacted the behavioral response during feeding. Under natural conditions the two populations feed on items differing in hardness and mobility, one being insectivorous (specialist) and the other one omnivorous (generalist). Our results suggest that these prey characteristics influence the way individuals modulate their jaw movements, especially the gape and the opening speed. Prey mobility also seems to be associated with an increase in the behavioral repertoire, probably because of the unpredictability of the prey movements. Most importantly, our results suggest that the individuals from the generalist population, characterized by a greater trophic breadth, showed greater behavioral flexibility in response to a change in prey type. Also, they showed an increased movement stereotypy, suggesting a finer motor control in the generalist population. Since the individuals included in the present study were kept in captivity and fed solely with crickets for a year and a half preceding the experiment, we suspect that these traits are hard-wired and may be under selection. The adaptive nature of observed differences in feeding kinematics that underly feeding specialization would be worth investigating in the future.

Data availability statement

The authors commit to make data available online upon acceptance of the manuscript.

Acknowledgements

We want to thank Hugues Clamouze for his precious help in designing and building the experimental set-up, Khalid Etefia for keeping the animals in good health, and team at Zoo Zagreb for maintaining them in captivity. Sampling of animals and maintenance in the Zoo of Zagreb was funded by Croatian Science Foundation grant HRZZ-IP-06-2016-9177. This work was made possible through the help of Tyson Hedrick from the University of North Carolina who helped us with the calibration of the cameras. The authors declare no conflict of interest.

References

- Arnold, S.J., 1983. Morphology, performance and fitness. *Am. Zool.* 23, 347–361.
- Bels, V.L., 1990. Quantitative analysis of prey-capture kinematics in *Anolis equestris* (Reptilia: Iguanidae). *Can. J. Zool.* 68, 2192–2198.
- Bolnick, D.I., 2001. Intraspecific competition favours niche width expansion in *Drosophila melanogaster*. *Nature* 410, 463–466.
- Bramble, D.M., Wake, D.B., 2013. Feeding mechanisms of lower tetrapods. In: *Functional vertebrate morphology*. Harvard University Press, pp. 230–261.
- Broeckhoven, C., Mouton, F.N., 2013. Influence of diet on prehension mode in cordylid lizards: a morphological and kinematic analysis. *J. Zool.* 291, 286–295.
- Brown, R.P., Perez-Mellado, V., 1994. Ecological energetics and food acquisition in dense Menorcan islet populations of the lizard *Podarcis lilfordi*. *Funct. Ecol.* 8, 427–434.
- Curtis, N., Jones, M.E.H., Evans, S.E., O'Higgins, P., Fagan, M.J., 2009. Visualising muscle anatomy using three-dimensional computer models – an example using the head and neck muscles of *Sphenodon*. *Palaeontol. Electron.* 12, 1–18.
- Donihue, C.M., Brock, K.M., Fofopoulos, J., Herrel, A., 2016. Feed or fight: testing the impact of food availability and intraspecific aggression on the functional ecology of an island lizard. *Funct. Ecol.* 30, 566–575.
- Herrel, A., De Vree, F., 2009. Jaw and hyolingual muscle activity patterns and bite forces in the herbivorous lizard *Uromastyx acanthinurus*. *Arch. Oral Biol.* 54, 772–782.
- Guillermé, T., 2018. dispRity: A modular R package for measuring disparity. *Methods in Ecology and Evolution* 9, 1755–1763.
- Hedrick, T.L., 2008. Software techniques for two- and three-dimensional kinematic measurements of biological and biomimetic systems. *Bioinspir. Biomim.* 3, 034001.

- Herrel, A., Cleuren, J., De Vree, F., 1996a. Kinematics of feeding in the lizard *Agama stellio*. *J. Exp. Biol.* 198, 1727–1742.
- Herrel, A., Van Damme, R., De Vree, F., 1996b. Sexual dimorphism of head size in *Podarcis hispanica atrata*: testing the dietary divergence hypothesis by bite force analysis. *Netherlands J. Zool.* 46, 253–262.
- Herrel, A., Timmermans, J.P., De Vree, F., 1998. Tongue flicking in agamid lizards: morphology, kinematics, and muscle activity patterns. *Anatom. Rec.* 252, 102–116.
- Herrel, A., Spithoven, L., Van Damme, R., De Vree, F., 1999a. Sexual dimorphism of head size in *Gallotia galloti*: testing the niche divergence hypothesis by functional analyses. *Funct. Ecol.* 13, 289–297.
- Herrel, A., Verstappen, M., De Vree, F., 1999b. Modulatory complexity of the feeding repertoire in scincid lizards. *J. Comp. Physiol. A.* 184, 501–518.
- Herrel, A., Meyers, J.J., Nishikawa, K.C., De Vree, F., 2001. The evolution of feeding motor patterns in lizards: modulatory complexity and possible constraints. *Am. Zool.* 41, 1311–1320.
- Herrel, A., Huyghe, K., Vanhooydonck, B., Backeljau, T., Breugelmans, K., Grbac, I., Van Damme, R., Irschick, D.J., 2008. Rapid large-scale evolutionary divergence in morphology and performance associated with exploitation of a different dietary resource. *Proc. Natl. Acad. Sci.* 105, 4792–4795.
- Irschick, D.J., Meyers, J.J., Husak, J.F., Le Galliard, J.F., 2008. How does selection operate on whole-organism functional performance capacities? A review and synthesis. *Evol. Ecol. Res.* 10, 177–196.
- Itescu, Y., Schwarz, R., Meiri, S., Pafilis, P., 2017. Intraspecific competition, not predation, drives lizard tail loss on islands. *J. Anim. Ecol.* 86, 66–74.
- Kalioztopoulou, A., Adams, D.C., van der Meijden, A., Perera, A., Carretero, M.A., 2012. Relationships between head morphology, bite performance and ecology in two species of *Podarcis* wall lizards. *Evol. Ecol.* 26, 825–845.
- Kraklau, D.M., 1991. Kinematics of prey capture and chewing in the lizard *Agama agama* (Squamata: Agamidae). *J. Morphol.* 210, 195–212.
- Liem, K.F., 1978. Modulatory multiplicity in the functional repertoire of the feeding mechanism in cichlid fishes. I. Piscivores. *J. Morphol.* 158 (3), 323–360.
- Metzger, K.A., 2009. Quantitative analysis of the effect of prey properties on feeding kinematics in two species of lizards. *J. Exp. Biol.* 212, 3751–3761.
- Meyers, J.J., Herrel, A., Birch, J., 2002. Scaling of morphology, bite force and feeding kinematics in an Iguanian and a Scleroglossan lizard. In: Aerts, P., D'Août, K., Herrel, A., Damme, Van (Eds.), *Topics in Functional and Ecological Vertebrate Morphology*. Shaker Publishing, pp. 47–62.
- Montuelle, S.J., Herrel, A., Schaeerlaeken, V., Metzger, K.A., Mutuyeyezu, A., Bels, V.L., 2009. Inertial feeding in the teiid lizard *Tupinambis merianae*: the effect of prey size on the movements of hyolingual apparatus and the cranio-cervical system. *J. Exp. Biol.* 212, 2501–2510.
- Montuelle, S.J., Herrel, A., Libourel, P.A., Reveret, L., Bels, V.L., 2010. Separating the effects of prey size and speed on the kinematics of prey capture in the omnivorous lizard *Gerrhosaurus major*. *J. Comp. Physiol. A.* 196, 491–499.
- Montuelle, S.J., Herrel, A., Libourel, P.A., Daillie, S., Bels, V.L., 2012. Flexibility in locomotor-feeding integration during prey capture in varanid lizards: effects of prey size and velocity. *J. Exp. Biol.* 215, 3823–3835.
- Moran, C.J., Rzcuidlo, C.L., Carlowicz, R.M., Gerry, S.P., 2018. Stereotyped feeding behaviors of polyphenic bluegill sunfish. *J. Zool.* 305, 116–123.
- Pafilis, P., Meiri, S., Foufopoulos, J., Valakos, E., 2009. Intraspecific competition and high food availability are associated with insular gigantism in a lizard. *Naturwissenschaften* 96, 1107–1113.
- Perry, G., 1996. The evolution of sexual dimorphism in the lizard *Anolis polylepis* (Iguania): evidence from intraspecific variation in foraging behavior and diet. *Can. J. Zool.* 74, 1238–1245.
- Rafinesque Schmalz, C.S., 1810. Caratteri di alcuni nuovi generi e nuove specie di animali e piante della Sicilia. Sanfilippo, Palermo, pp. 105–pp.
- Ralston, K.R., Wainwright, P.C., 1997. Functional consequences of trophic specialization in pufferfishes. *Funct. Ecol.* 11, 43–52.
- Reilly, S., McBrayer, L.D., Miles, D.B., 2007. *Lizard Ecology. The Evolutionary Consequences of Foraging Mode*. Published by the Cambridge University Press, Cambridge, United-Kingdom.
- Sagonas, K., Pafilis, P., Lymberakis, P., Donihue, CM, Herrel, A., Valakos, ED, 2014. Insularity affects head morphology, bite force and diet in a Mediterranean lizard. *Biol. J. Linn. Soc.* 11, 469–484.
- Sanderson, S.L., 1988. Variation in neuromuscular activity during prey capture by trophic specialists and generalists (Pisces: Labridae). *Brain Behav. Evol.* 32, 257–268.
- Sanderson, S.L., 1990. Versatility and specialization in labrid fishes: ecomorphological implications. *Oecologia* 84, 272–279.
- Schaerlaeken, V., Herrel, A., Meyers, J.J., 2008. Modulation, individual variation and the role of lingual sensory afferents in the control of prey transport in the lizard *Pogona vitticeps*. *J. Exp. Biol.* 211, 2071–2078.
- Schaerlaeken, V., Montuelle, S.J., Aerts, P., Herrel, A., 2011. Jaw and hyolingual movements during prey transport in varanid lizards: effects of prey type. *Zoology* 114, 165–170.
- Schoener, T.W., 1977. Competition and the niche. *Biol. Reptilia* 7, 35–136.
- Schwenk, K., 2000. Feeding. In: *Form, Function, and Evolution in Tetrapod Vertebrates*. Published in the Academic Press, London, United-Kingdom.
- Schwenk, K., Throckmorton, G.S., 1989. Functional and evolutionary morphology of lingual feeding in squamate reptiles: phylogenetics and kinematics. *J. Zool.* 219, 153–175.
- Smith, T.L., Kardong, K.V., Bels, V.L., 1999. Prey capture behavior in the blue-tongued skink, *Tiliqua scincoides*. *J. Herpetol.* 33, 362–369.
- Taverne, M., Fabre, A.C., King-Gillies, N., Krajnovic, M., Lisicic, D., Martin, L., Michal, L., Petricioli, D., Stambuk, A., Tadic, Z., Vigliotti, C., Wehrle, B., Herrel, A., 2019. Diet variability among insular populations of *Podarcis* lizards reveals diverse strategies to face resource-limited environments. *Biol. J. Linn. Soc.* 9, 12408–12420.
- Taverne, M., King-Gillies, N., Krajnovic, M., Lisicic, D., Mira, O., Petricioli, D., Sabolic, I., Stambuk, A., Tadic, Z., Vigliotti, C., Wehrle, B., Herrel, A., 2020. Proximate and ultimate drivers of variation in bite force in the insular lizards *Podarcis melisellensis* and *Podarcis sicula*. *Biol. J. Linn. Soc.* 131, 88–108.
- Theriault, D.H., Fuller, N.W., Jackson, B.E., Bluhm, E., Evangelista, D., Wu, Z., Betke, M., Hedrick, T.L., 2014. A protocol and calibration method for accurate multi-camera field videography. *Methods and Techniques* 217, 1843–1848.
- Thomas, G.H., Meiri, S., Phillimore, A.B., 2009. Body size diversification in *Anolis*: novel environment and island effects. *Evolution* 63, 2017–2030.
- Van Damme, R., 1999. Evolution of herbivory in Lacertid lizards: effects of insularity and body size. *J. Herpetol.* 33, 663–674.
- Van Wassenbergh, S., Herrel, A., Adriaens, D., Aerts, P., 2006. Modulation and variability of prey capture kinematics in clariid catfishes. *J. Exp. Zool. Part A.* 305, 559–569.
- Verwajen, D., Van Damme, R., Herrel, A., 2002. Relationships between head size, bite force, prey handling efficiency and diet in two sympatric lacertid lizards. *Funct. Ecol.* 16, 842–850.
- Wainwright, P.C., Bennett, A.F., 1992. The mechanism of tongue projection in chameleons: I. Electromyographic tests of functional hypotheses. *J. Exp. Biol.* 168 (1), 1–21.
- Wainwright, P.C., Mehta, R.S., Higham, T.E., 2008. Stereotypy, flexibility and coordination: key concepts in behavioral functional morphology. *J. Exp. Biol.* 211, 3523–3528.
- Wöhl, S., Schuster, S., 2007. The predictive start of hunting archer fish: a flexible and precise motor pattern performed with the kinematics of an escape C-start. *J. Exp. Biol.* 210, 311–324.
- R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: <https://www.R-project.org/>.