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„*Eublepharis macularius*“

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Show me how you eat, and I tell you how your skull moves - Cranial kinesis of the leopard gecko „*Eublepharis macularius*“

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Contents

Abstract

Looking at the intracranial movements during food consumption, one speaks about cranial kinesis. These movements within the skull of vertebrates occur independently of the mandible, the middle ear and the hypobranchial skeleton. Regarding these movements, there are some main terms related to the cranial kinesis of Squamata including mesokinesis, metakinesis, amphikinesis and streptostyly. The present study investigated intracranial movements in the gecko *Eublepharis macularius*. Looking on morphological and experimental data based on high speed cinematography and 3D visualization of microCT scans and image segmentation, we compared two adult males, two adult females and two subadults (male and female) while fed with two different prey items (*Acheta domesticus* and the wax moth larvae of *Galleriinae*). Mesokinesis was detected through high speed cinematography in all three groups with both prey items during prey capture, oral manipulation and transportation. The data moreover indicate a high potential for amphikinesis and streptostyly. The comparison between the prey items showed differences in the duration and speed of the feeding cycle. In addition, the two prey items affect differently the intracranial movement patterns. Comparing the three groups, the subadults showed the highest flexibility at the fronto-parietal suture (mesokinetic angle). Variations between the three groups regarding the speed and duration of each cycle could be detected too. The muscle volume analysis showed that the external and posterior adductor muscles, form together the biggest muscle in the skull. Allover, the presented data show a that *E. macularius* is a highly kinetic species within the basal group of Gekkota.

Introduction

In vertebrates food consumption generally means that external food resources get ingested intraorally to be transformed into vital energy and nutrients. This serves to ensure survival and reproduction (Hildebrand, & Goslow, 2004). Due to several environmental pressures and evolutionary patterns the skulls of the different vertebrate lineages split into akinetic skulls and kinetic skulls. On the one hand, mammals, for example, have akinetic skulls with only the lower jaw articulating and middle ear rotation within the skull. These classes evolved strong interdigitating sutures between bones which don't permit any other intercranial mobility (Werneburg & Maier, 2019). On the other hand, the evolution of prey capture in squamates is linked to the behaviour of lingual or jaw prehension. Typically, species using lingual prehension like Iguania show an akinetic skull, whereas species capturing with jaw prehension may show intercranial movements (for review see: Metzger, 2002; Handschuh et al., 2019; Ollonen et al., 2018). This mobility requires some cranial movement patterns that must be performed dynamically and in a coordinated manner for successful feeding. This pattern is defined as the coordination in time and amplitude of movement (Wainwright et al., 2008).

Focusing on the cranial movements during food consumption, we speak about cranial kinesis. These movements within the skull of vertebrates, occur independently of the mandible, the middle ear and the hypobranchial skeleton (for review see: Frazzetta, 1962, 1983, 1986). The diversity of food capturing and consumption and the duration of the whole feeding cycle (defined from the beginning of the prey capture till the swallowing of the prey into the esophagus) can't be more varying within lizards, however the feeding cycle can (most of the time) be subdivided into three types of gape cycles (see method/terminology). Frazetta developed in 1962 the so called "quadric-crank"-model for the intracranial movement patterns of squamates during mouth opening and closing within the entire feeding process. Following Frazettas opinion, which was based on an earlier work by Versluys, 1910, 1912, 1936, there are some main terms related to the cranial kinesis of Squamata: (1) Streptostyly, the pendulum-like rotational movement of the quadrate about its dorsal articulation point on the chondrocranium which allows the position of the jaw joint to move forward and backward. The movement of the quadrate also results in a shifting of the temporo-mandibular joint(T. H. Frazzetta, 1962). (2) Prokinesis (only in birds and snakes), which describes a joint at the naso-frontal region in front of the eye (orbit); (3) Mesokinesis, which is the dorsal extension and ventral flexion of the snout around a transverse axis (fronto-parietal suture) behind the eye (orbit); (4) Metakinesis, a movement of the cranial roof (dermatocranium) against the occipital region (chondrocranium). (5) The simultaneous presence of mesokinesis and metakinesis is termed as amphikinesis. Variations of these types exist in a wide variety of forms and evolutionary adaptations, such as pure streptostyly or streptostyly in combination with mesokinesis or metakinesis (for review see: Frazzetta, 1962, 1986 and Metzger, 2002).

With respect to tetrapods, investigations on cranial kinesis have been conducted especially in extant Sauropsida (non-ophidian squamates, ophidians/snakes and birds) (Vincent Bels et al., 2019; Moon et al., 2019; Rico-Guevara et al., 2019). Joints within the kinetic skull of sauropsids allow the snout to lift upward or bend downward due to the mesokinetic articulation independently from the rest of the dermatocranium. This leads to a change in the angle of closure of the teeth and so both rows close directly on the prey. This has a functional significance for the hunting success (capture phase) and so for the surviving of the animal (For review see: Kardong, 2012). In particular, streptostyly and mesokinesis have been described in several squamates and can be detected by high speed imaging and CT scans (Handschuh et al., 2019; Herrel et al., 1999, 2007; Montuelle & Williams, 2015). In addition, there is the assumption that juvenile stages often have higher kinetics than the adult stages (Barahona & Barbadillo, 1998; Starck, 1979). On the other side, metakinesis cannot be detected by high speed recordings, as the movements cannot be observed superficially. The evolutionary and functional adaptations of this high variety of cranial kinesis have been experimentally investigated in many different suborders of squamates and researched for possible explanatory patterns for specific

evolutionary advantages(For review see: Metzger, 2002). The most important fact seems to be, that the angle change in the fronto-parietal suture while feeding guarantees a higher success in capturing and in maintaining the prey.

The evolutionary developments of the skull within the superorder Lepidosauria show a linear trend towards the loss of cranial elements (Herrel et al., 2007). Some squamates (*Gekkota* and *Varanidae*) lost independently the postorbital arch, which is the connection between the jugal and the skull roof. This loss allows for greater cranial mobility and flexibility (Herrel et al., 2007). In addition, *Gekkota* have also experienced a reduction of the supraorbital arch, thereby increasing the possible flexibility (Herrel et al., 2007). The cranial morphology of *Eublepharis macularius* shows a lightweight construction and the jugal is completely reduced, as in all *Gekkota* (Herrel et al., 2007). Since the postorbital arch is reduced and the orbita is enlarged, the postorbital region is pushed more in caudal direction and reduced in size (Herrel et al., 2007). The quadrate is long and also relatively broad and provides a large, strong and well-developed musculature for feeding (M. adductor mandibulae posterior). Based on these morphological data the aim of this study is (1) to analyze the feeding mechanisms of the leopard gecko *Eublepharis macularius* with special emphasis on the functional morphology of the major parts of the feeding apparatus involved in cranial kinesis, (2) to investigate, if the provided food items change the feeding kinematics of this animals, (3) if they show a sexual dimorphism and (4) to analyze if the juvenile (subadult) stages show higher kinetics than the adult stages and therefore support the thesis of Stark (1979) and Barahona and Barbadillo (1998).

The leopard gecko (*Eublepharis macularius*) belongs to the gekkotan within the order of the Squamata. They are sturdily build, have a spotted coloration (like the leopard, *Panthera pardus*) and are therefore perfectly adapted to their habitat in the dry grassland and desert regions of southwest Asia (Afghanistan, Iran, Pakistan, India, and Nepal). Being ground dwellers, all members of the family *Eublepharidae* have toes without adhesive lamellae (common for other gekkotan). They are nocturnal predators and the variety of their diet reaches from invertebrates to small vertebrates (in captivity). These animals are visual hunters, therefore their eyes are enlarged and have two movable eyelids (Grießhammer & Köhler, 2006; Henkel & Schmidt, 2009). Females and males show a sexual (male-biased) dimorphism in size. The males are more strongly built with significant larger heads and pronounced preanal pores (Kratochvíl & Frynta, 2002).

Methods

Terminology

In this work the terminology introduced by Versluys (1912, 1936) and specified by Frazzetta (1962) is used for the definitions of the different ways of kinetic movement in the skull (see above).

The feeding cycle can (most of the time) be subdivided into three types of gape cycles (excluding the swallowing). The capture of the prey (ingestion) is described as the approach of the predator to the prey until the first bite (Montuelle et al., 2009, 2012; Montuelle & Kane, 2019). This is followed by two alternating phases, the twisting and turning of the prey with the tongue, the so called "manipulation"-phase and the "transport"-phase in which the prey is brought further backwards into the intraoral area (Montuelle & Kane, 2019) as preparation for the swallowing process. Bels (2003) suggested to define the capture, manipulation and transportation cycles of all tetrapod's in terms of specific phases which are defined by their variable speed. Each cycle shows the classical division in a so called slow opening phase (SO), fast opening phase (FO), fast closing phase (FC) and a slow closing phase combined with a power stroke phase (PS).

Animals

A total number of four adults (seven to nine year old) and two subadults (three year old) *Eublepharis macularius* individuals were used in this study. Each age level with an equal quantity of females and males (in total three males and three females). The individuals were, for the time of the experimental part of the study, provided by a private owner. No experiment required an invasive method or did in any way affect negatively the animals. No animal was forced to cooperate during the experiment. Keeping of the animals at the University of Vienna and filming of feeding events was allowed by the council of animal protection of the Faculty of Life Sciences (Ref.No.: 2019-005).

Measurements

All animals were measured in snout-vent length (SVL), and head length, width and height. The snout-vent length was measured manually by measuring from the tip of the snout to the beginning of the tail (behind the cloaca). The head length, width and height were measured within the recorded videos using a MATLAB based tracking software (see below). The length was measured from the very tip of the snout to behind the tympanum. The height was measured from the fronto-pariental suture in a perpendicular to the lower jaw and the width was measured through the distance between the tympanum regions.

High speed cinematography

High speed video recordings of food consumption (capture, intraoral manipulation and transportation) of all six animals were done in a film aquarium (30x15x15cm) with a reference scale grid for later calibration (10mm) (see figure 1). To compare two different prey items, the animals were fed during the experiments with house crickets (*Acheta domesticus*) and wax moth larvae (*Galleriinae*). The size of these feed animals were chosen according to the body-size of the recorded animal (see table 1). The videos were recorded using a Photron FASTCAM Mini Ax100 high speed camera (Photron, San Diego, CA, USA) equipped with a Micro-lens Tamron SP 24-70 mm F/2.8 (Tamron Co. Ltd., Saitma, Japan). Three LED-lights (Neewer LED Ringlight, ESDDI LED videolight, LED Spot) ensured adequate illumination and thus high quality resolution. The resulting videos were immediately edited with the software Photron FASTCAM Viewer, v4.0.5.0. All the videos were recorded at 500 fps (frames/s). The animals were consistently filmed in a lateral view while feeding. In total, more than 120 feeding events (40 with wax moth larvae and about 80 with house crickets) were filmed, but only 90 films could be used for further analyses.

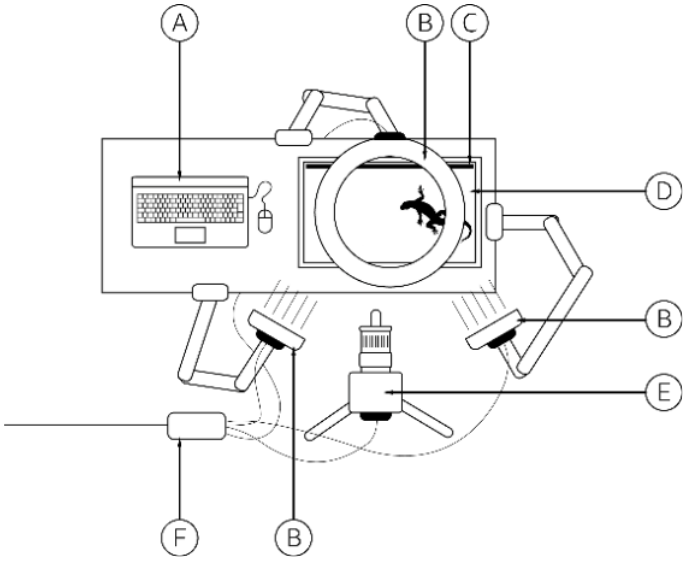


Figure 1 Methodological set-up. (A) Laptop with the software Phroton FASTCAM Viewer v4.0.5.0; (B) light sources; (C) background; (D) film terrarium; (E) Phroton FASTCAM Mini Ax100; (F) Power source

The approach to the prey marked the beginning of the feeding cycle; it started, when the individual made quick and direct movements towards the prey and ended, when the tip of the snout reached (touched) the prey. The feeding cycle was then divided into the (i) capture phase, noted from the first opening of the individual's mouth to the first closing of the mouth and therefore the capture of the prey; the (ii) oral manipulation phases, and the (iii) oral transportation phases. With respect to feeding house crickets, for each animal the best 10 capture phases, 20 manipulation phases (two per feeding event) and 20 transport phases (two per feeding event) were chosen. For the wax moth larvae feeding

events only 4 capture phases, 8 transport and manipulation phases could be analyzed. The wax moth larvae have a high fat content and are therefore, in large quantities, unhealthy for the leopard geckos. For this reason only half as many wax moth larvae were fed than crickets. In addition, the two "manipulation" and "transport" phases of each feeding cycle where differentiated into "manipulation_1" for a manipulation phase in the beginning and "manipulation_2" for a manipulation phase in the later part of the feeding cycle. The same was done with the transport phases. All the video sequences were analyzed with a custom motion tracking program (designed by C. Beisser and P. Lemell; programmed by C. Beisser) developed in MATLAB R2015b (MathWorks, Inc., Natick, MA, USA), which uses predictive algorithms based on a digitizing software that was implemented in MATLAB by Hedrick (2008). Further analyses were performed with custom MATLAB scripts built in MATLAB R2015b.

For a general analysis of the feeding cycles, the x-y coordinates of two tracking points were tracked frame by frame in all videos. One point marked the tip of the upper jaw and the second point the tip of the lower jaw. The evaluation of the two points enabled an exact analysis of the movement patterns. Two more points marked the prey item and a reference point on the animal itself. Based on these points, the following variables were determined: (i) duration and velocity of the approach (mean velocity and the mean of the five highest velocities (max. vel. (5)); (ii) duration, mean velocity and max. vel. (5) of the subdivided examined phases (SO, FO, FC, PS) of each gape cycle (capture, 2x manipulation, 2x transport); (iii) the mesokinetic angle (the angle between the frontal and parietal at the fronto-parietal suture) was measured at the end of every single phase in all gape cycles (see figure 2 – capture cycle FO phase).

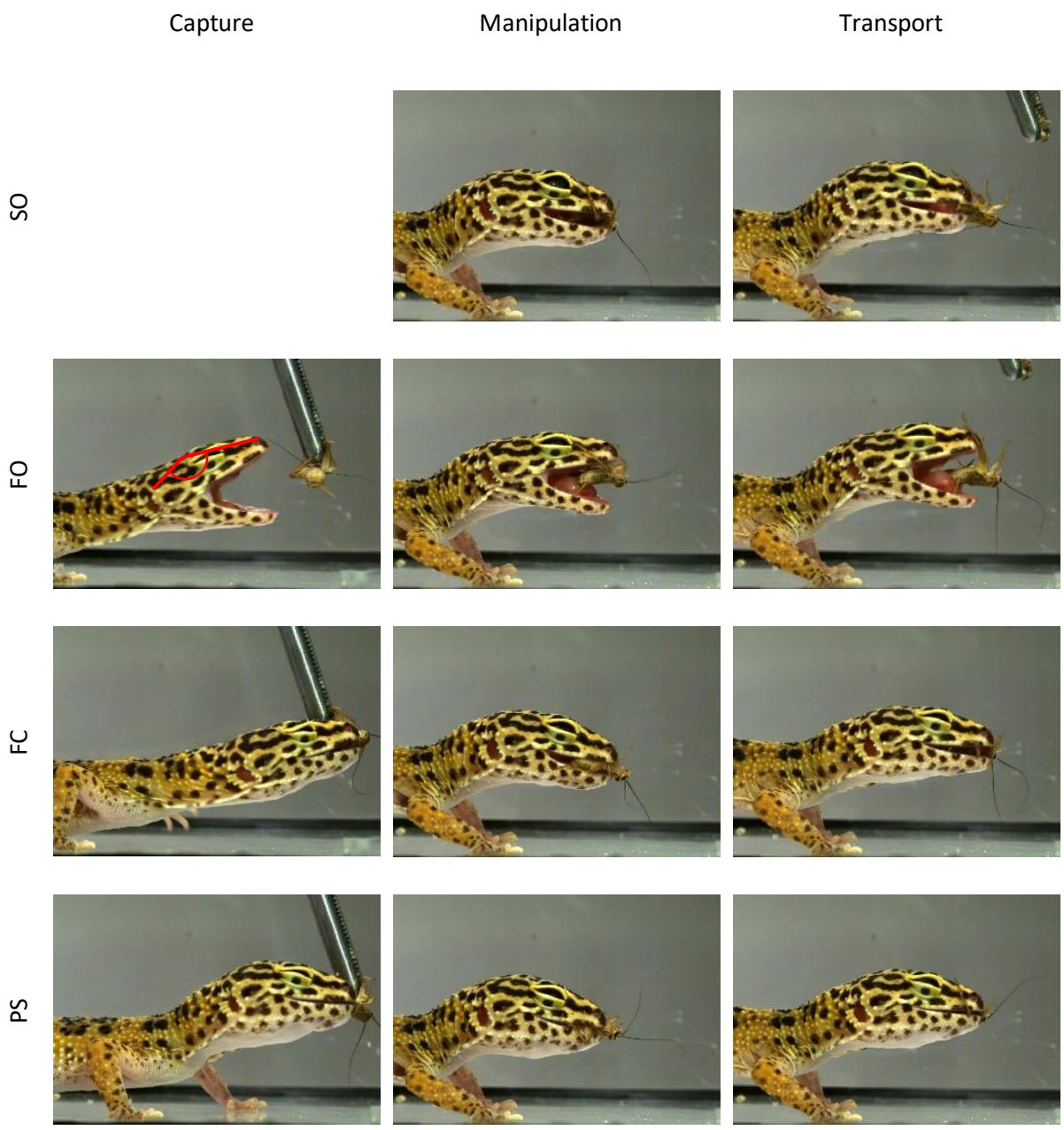


Figure 2 Feeding cycle of Eublepharis macularius. *Representing capture, manipulation and intraoral transport cycle. Each gape cycle is defined by four specific time points during the cycle: the slow opening phase (SO) (except capture), fast opening (FO), fast closing (FC) and the power stroke (PS) phase.*

Table 1 Defined prey item size

Individual (SVL in cm)	**Prey item**	**Length of prey (in cm)**
>13	*Acheta domesticus*	1,6 - 2,1
<13	*Acheta domesticus*	1,1 - 1,5
>13	larva of *Galleriinae*	2,8 - 3,2
<13	larva of *Galleriinae*	2,3 - 2,7

3D visualisation of microCT scans

For this study two adult males with a closed mouth were provided by the Naturhistorisches Museum Wien (NHM). Two scans were done, one only for the bone structure (NHM 18050), and one for a dual energy scan (NHM 38233:2) to include the musculature structure. For the second scan the male was dehydrated to absolute ethanol, stained with 1% elemental iodine in ethanol for 7 days, washed in absolute ethanol, and scanned with an isotropic voxel resolution of 7µm.

The 3D visualizations of the skull of *Eublepharis macularius* were made using volume rendering in the Software Drishti 2.4 (LIMAYE, 2012). The data was generated in 2019 by Stephan Handschuh at the Vetmed University Vienna and provided by the data owner Patrick Lemell. They were scanned with a Zeiss XRadia MicroXCT-400 scanner (Carl Zeiss X-ray Microscopy, Pleasanton, CA) at 70kVp/114µA.

The dual energy scan was again done by Stephan Handschuh at the Vetmed University Vienna in 2022. It was scanned with a XRadia MicroXCT-400 (Carl Zeiss X-ray Microscopy, Pleasanton, CA, USA). The low energy scan was done with 40kVp/200µA and the high energy scan with 80kVp/100µA (X-Ray filter: Zeiss LE#4) with an exposure time per projection of 20s for the 40kVp Scan and 10s for the 80kVp scan. The angular increment between projections was 0.225° and the voxel size 16.12µm isotropic.

Image segmentation and measurement of muscle volumes

The dual microCT image volumes of the skull were imported into the 3D software package Amira [FEI SAS, Mérignac, France (part of Thermo Fisher Scientific)]. Muscles involved in mouth opening and closing were segmented and visualized. Additionally, the segmented muscle volumes were measured. The shown volumina don't exactly represent the in vivo volumina, as the method of conservation shrinked the muscle material of about 20-30% from their original size.

Statistical Analysis

Analysis of variance (ANOVA) was used to test the three groups (males, females and subadults) for the H_0 hypothesis and possible significances. The H_0 hypothesis assumes that there were no differences between the groups. This was done for time measurements, speed measurements and angle measurements in all described phases of all cycles.

Each group was then tested for possible differences between the two prey options (*A. domesticus* and *Galleriinae*) using T-test analysis for significances and the Bonferroni post hoc analysis for pairwise comparison. To test whether the samples have the same variance or not, in all cases the Levene test was used.

Results

Animals

The adult males (7 and 9 year old) are bigger in their absolute body length then the equally old adult females. The subadult female (3 year old) had a bigger body length, but the head was more or less the same size as the one from the subadult male. For more detail see table 2.

Table 2 Body measurements of all tested animals of Eublepharis macularius *in mm*

Individual	Body length	Head length	Head width	Head height
3 Year old male	105	19,1	6,1	8,7
3 Year old female	120	19,7	6,5	9,1
7 Year old male	155	22,6	8,2	10,1
7 Year old female	140	23,4	7,9	10,1
9 Year old male	165	23,7	9,7	10,3
9 Year old female	145	22,8	8,2	9,3

Video-analysis

The approach to the prey indicates the beginning of a feeding cycle. Thereby, the leopard gecko focuses the prey patiently and moves slowly in reach distance. Then the individual moves with the entire front body parts (but without moving the anterior legs) with high speed forward (= approach) and smoothly changes into the capture cycle. The individual opens the mouth widely and (in best case) catches the prey by jaw prehension. This capture cycle (see figure 3, 1. peak) is especially marked by the absence of a slow opening phase and the largest distance between the upper and lower jaw at the maximum of mouth opening (y-axis). The capture cycle is mostly (but not always) followed by a manipulation cycle (2. peak) with an extended slow opening phase and a prominent power stroke. After one or two manipulation cycles, a transport cycle follows. In this example the transport cycle (3. peak) is marked by a higher mouth opening than in the manipulation phase and only a notable power stroke. Manipulation and transport cycle can alternate. Manipulation and transport cannot exclusively be detected by the graph of a feeding cycle, only by comparing it with the recorded video one can definitely say, if a cycle is a manipulation or a transport cycle. The quantity and order of manipulation and transport cycles is depending on the prey size and the initial capture (the position of the prey within the mouth).

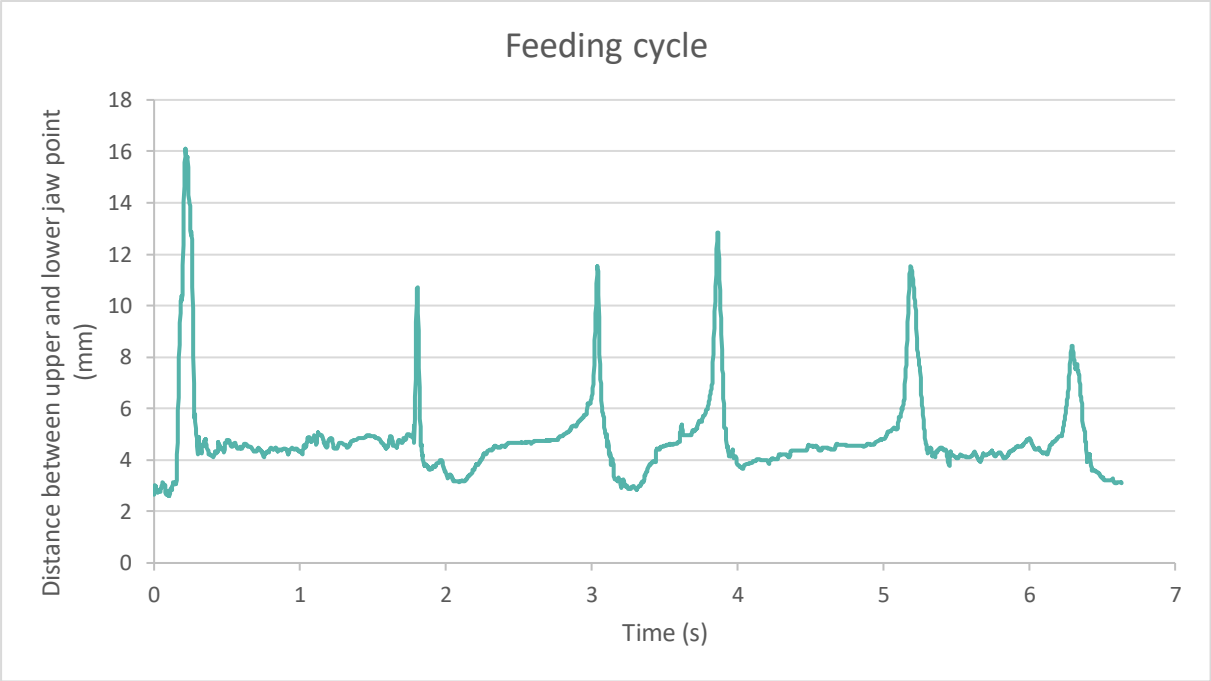


Figure 3 Example of an entire feeding cycle of Eublepharis macularius. *Food consumption of* Acheta domesticus *by an adult female.*

Statistical analysis

Approach to the prey

Approach – Acheta domesticus

The mean duration of the approach to the cricket *Acheta domesticus* is in all three groups (males, females and subadults) around 0,1s. Also the mean velocity and the max. vel. (5) of all three groups during the approach to the prey is similar to each other (see table 3).

Table 3 Approach to the prey (Acheta domestica). Duration in s, mean velocity and max. vel. (5) in mm/s. N=10

Approach	**Males**		**Females**		**Subadults**	
	mean	SD	mean	SD	mean	SD
Duration	0,142	0,061	0,115	0,029	0,130	0,063
mean velocity	216,020	105,549	189,226	44,514	185,283	111,930
max. vel. (5)	434,278	186,371	428,961	125,651	395,603	206,744

A factorial analysis of variance showed that there is no significant difference between the categories of the variable “Group” (males, females, subadults) in relation to the variable duration, mean Velocity and max. vel. (5). With these data, the null hypothesis is thus not rejected.

Approach – Galleriinae

The mean duration of the approach to the wax moth larvae *Galleriinae* shows similarity in all three groups. The mean velocity of the males during the approach seems higher, than the ones of the females and subadults, but it has an extremely high SD. The same also applies for the max. vel. (5) of the subadults (see table 4).

Table 4 Approach to the prey (Galleriinae). Duration in s, mean velocity and max. vel. (5) mm/s. N=4

Approach	**Males**		**Females**		**Subadults**	
	mean	SD	mean	SD	mean	SD
Duration	0,154	0,062	0,165	0,048	0,234	0,191
mean velocity	159,452	127,340	108,397	41,069	110,415	84,752
max. vel. (5)	267,230	98,901	251,628	81,160	302,787	136,611

A factorial analysis of variance showed that there is no significant difference between the categories of the variable “Group” in relation to the variable duration, mean Velocity and max. vel. (5). With these data, the null hypothesis is thus not rejected

Approach- statistical analysis

Comparing the duration, the mean velocity and the max. vel. (5) of the two different prey items consumed by the **males** following observations can be made: The Levene test of variance equality, for the dependent variable “duration”, yields a p-value of 0.729, which is above the significance level of 5%. The Levene test is therefore not significant and the null hypothesis (h_0) that all variances of the groups are equal is retained. The two-tailed t-test for independent samples was not statistically significant.

The mean velocity shows similar results. The Levene test of variance equality, for the dependent variable “mean Velocity”, yields a p-value of 0.573, which is above the significance level of 5%. The Levene test is therefore again not significant and the h_0 is retained. The two-tailed t-test for independent samples was not statistically significant.

The Levene test of variance equality for the dependent variable “max. vel. (5)” yields a p-value of 0.06, which is slightly above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. The two-tailed t-test for independent samples (equal variances tested by the Levene-test) showed that the difference between the *Acheta domesticus* and *Galleriinae* with respect to the dependent variable “max. vel. (5)” was statistically

significant, t(26) = -2.32, p = 0.029, 95% confidence interval [-315.34, -18.75]. The h_0 is thus rejected. (*Acheta domestcus* > *Galleriinae*)

Comparing the duration, the mean velocity and the max. vel. (5) of the two different prey items consumed by the **females** following observations can be made: The Levene test of variance equality, for the dependent variable "duration", yields a p-value of 0.132, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. The two-tailed t-test for independent samples (equal variances assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable duration was statistically significant, t(26) = -3.25, p = 0.003, 95% confidence interval [-0.08, -0.02]. The h_0 is thus rejected. (*Galleriinae* > *Acheta domesticus*)

The Levene test of variance equality, for the dependent variable "mean Velocity", yields a p-value of 0.901, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. Thus, there is equality of variance in the samples. The two-tailed t-test for independent samples (equal variances assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable "mean Velocity" was statistically significant, t(26) = 4.27, p = <0.001, 95% confidence interval [41.95, 119.71]. The h_0 is thus rejected. (*Acheta domestcus* > *Galleriinae*)

The Levene test of variance equality, for the dependent variable "max. vel. (5)", yields a p-value of 0.388, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. The two-tailed t-test for independent samples (equal variances assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable "max. vel. (5)" was statistically significant, t(26) = 3.56, p = 0.001, 95% confidence interval [74.94, 279.72]. The h_0 is thus rejected. (*Acheta domestcus* > *Galleriinae*)

Comparing the duration, the mean velocity and the max. vel. (5) of the two different prey items consumed by the **subadults** following observations can be made: The Levene test of variance equality, for the dependent variable "duration", yields a p-value of 0.008, which is below the significance level of 5%. The Levene test is therefore significant and the h_0 that all variances of the groups are equal is rejected. The two-tailed t-test for independent samples showed that the difference between the *Acheta domesticus* and *Galleriinae* with respect to the dependent variable duration was not statistically significant, t(8,1) = -1.41, p = 0.195, 95% confidence interval [-0.21, 0.05]. The h_0 is thus retained.

The Levene test of variance equality, for the dependent variable “mean Velocity”, yields a p-value of 0.042, which is below the significance level of 5%. The Levene test is therefore significant and the h_0 that all variances of the groups are equal is rejected. The two-tailed t-test for independent samples showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable “mean Velocity” was not statistically significant, t(16,07) = 2.04, p = 0.058, 95% confidence interval [-3.2, 168.18]. The h_0 is thus retained.

The Levene test of variance equality, for the dependent variable “max. vel. (5)”, yields a p-value of 0.004, which is below the significance level of 5%. The Levene test is therefore significant and the h_0 that all variances of the groups are equal is rejected. The two-tailed t-test for independent samples (equal variances not assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable “max. vel. (5)” was not statistically significant, t(21.86) = 1.54, p = 0.139, 95% confidence interval [-35.97, 240.62]. The h_0 is thus retained.

Feeding cycle

Visualization of the feeding cycle

The peak of the capture cycle is in all three groups and with both prey-types always the highest. In both prey situations, the adult males show a higher peak in the capture cycle than the adult females and the subadults. The subadults show in all cycles of both prey smaller peaks in contrast to the adult males and slightly smaller peaks in contrast to the adult females. There is no notable difference between the height of the peak of the manipulation 1&2 cycle and the transport 1&2 cycle. Only the SO phase shows some differences. The feeding cycles of the *Galleriinae* show always smaller gape openings than the one of *Acheta domesticus*. There is no notable difference between the height of the peak of the manipulation 1&2 cycle and the transport 1&2 cycle between the three groups. Only the SO phase shows some differences. The feeding cycles of the Galleriinae show always smaller gape openings than the one of Acheta domesticus. In both prey types the manipulation_2 has in all three groups a lower peak than manipulation_1, same is true for transport_2 and transport_1 (see figure 4 and figure 5)

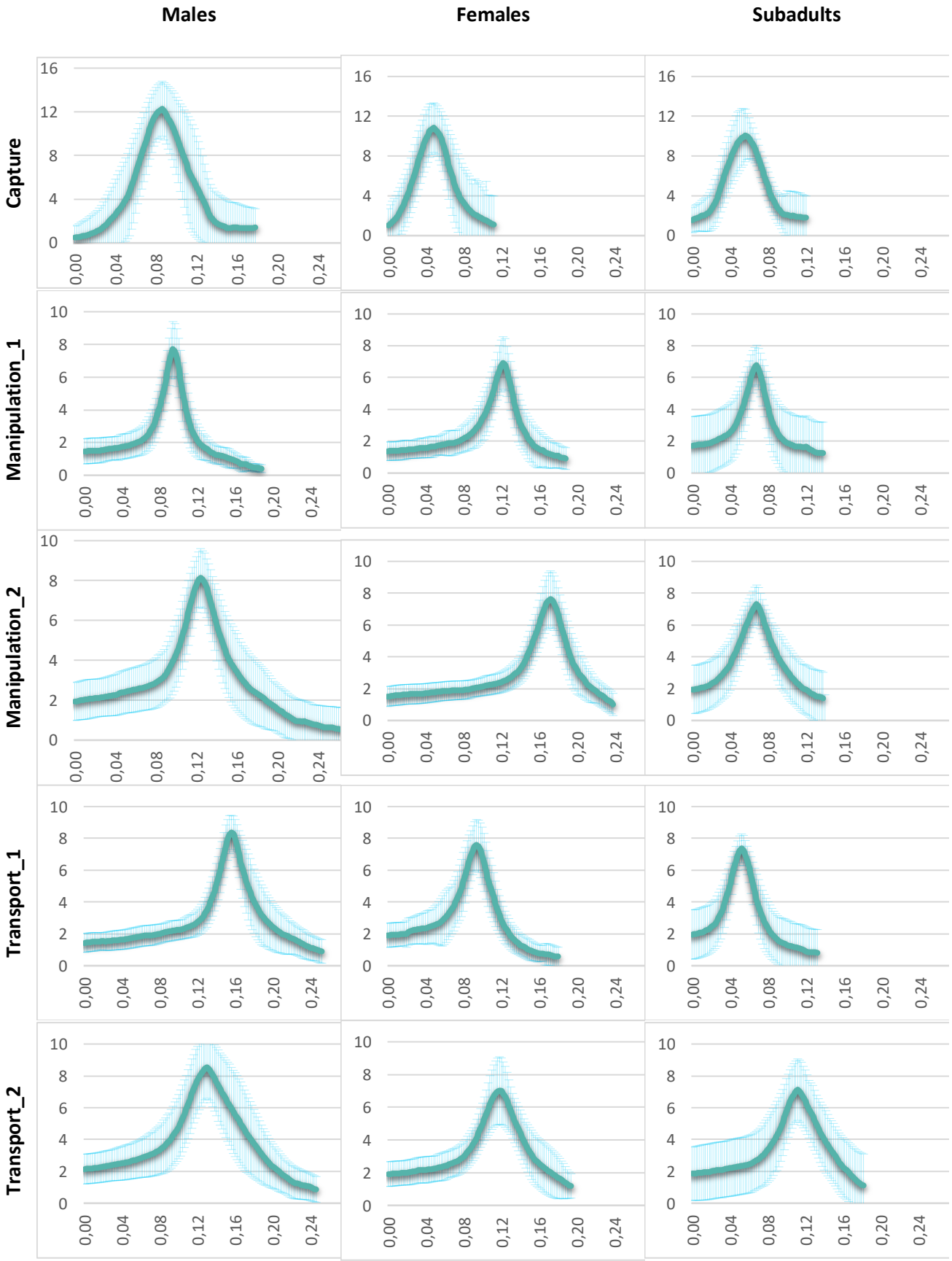


Figure 4 Gape cycle kinematics of Eublepharis macularius *during food consumption of* Acheta domesticus. *Representation of the mean curve of males, females and subadults during capture, manipulation (1+2) and transport (1+2). (time) x-axis in s and (distance) y-axis in mm. (N=10)*

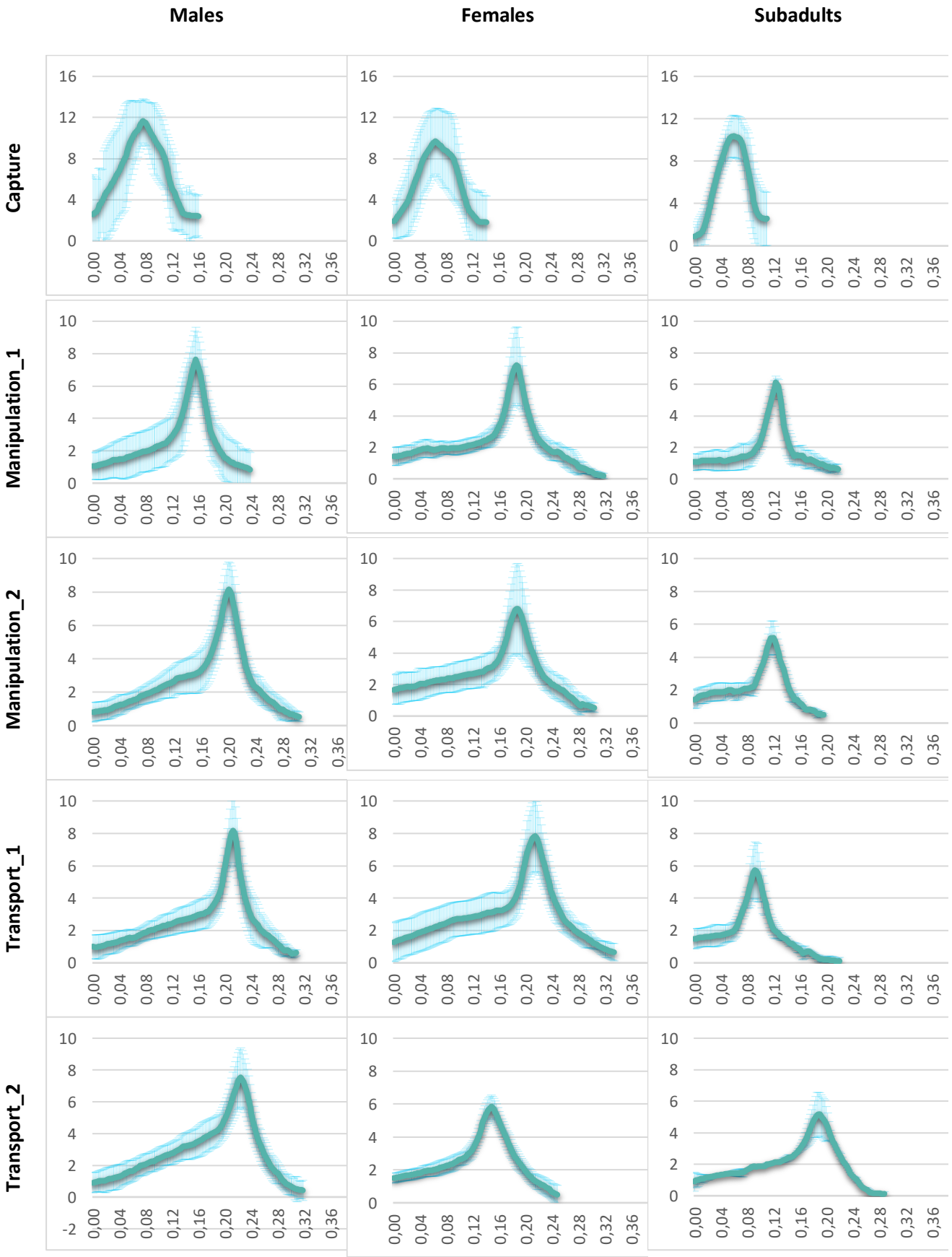


Figure 5 Gape cycle kinematics of Eublepharis macularius *during food consumption of* Galleriinae. *Representation of the mean curve of males, females and subadults during capture (N=4), manipulation (1+2) and the transport (1+2). (time) x-axis in s and (distance) y-axis in mm. (N=8)*

Duration and Velocity

Duration, mean velocity and max. vel. (5) – Acheta domesticus

As in the visualization of the feeding cycles (figure 4 and figure 5) observed, the data from table 5 present similar patterns. The longest duration of each cycle is always the SO phase. This relates to all three groups. The FO and FC phases show similar duration times in each cycle (capture, manipulation and transportation) of each group. In the capture cycle of all groups, the FC phase is faster than the FO phase, whereas in all other cycles FC and FO show similar speeds. (see table 5)

Table 5 Duration (s), mean velocity (mm/s) and max vel. (5) (mm/s) of all phases of the feeding cycle of Eublepharis macularius. *Consumption of* Acheta domesticus. *(N=10)*

Duration	**Males**		**Females**		**Subadults**	
Phase	mean	SD	mean	SD	mean	SD
FO_Capture	0,062	0,029	0,046	0,010	0,056	0,025
FC_Capture	0,042	0,017	0,038	0,019	0,035	0,022
PS_Capture	0,052	0,054	0,042	0,044	0,076	0,057
SO_Manipulation_1	0,142	0,099	0,121	0,089	0,135	0,247
FO_Manipulation_1	0,032	0,012	0,037	0,033	0,046	0,083
FC_Manipulation_1	0,028	0,009	0,032	0,017	0,043	0,076
PS_Manipulation_1	0,065	0,033	0,062	0,038	0,090	0,130
SO_Manipulation_2	0,179	0,094	0,163	0,090	0,082	0,055
FO_Manipulation_2	0,043	0,009	0,051	0,030	0,037	0,008
FC_Manipulation_2	0,054	0,028	0,047	0,020	0,042	0,026
PS_Manipulation_2	0,083	0,046	0,063	0,040	0,062	0,043
SO_Transport_1	0,202	0,109	0,184	0,156	0,133	0,245
FO_Transport_1	0,040	0,013	0,033	0,011	0,047	0,071
FC_Transport_1	0,051	0,025	0,037	0,015	0,054	0,102
PS_Transport_1	0,085	0,054	0,065	0,042	0,066	0,090
SO_Transport_2	0,191	0,123	0,190	0,115	0,136	0,093
FO_Transport_2	0,051	0,022	0,050	0,016	0,067	0,101
FC_Transport_2	0,072	0,033	0,059	0,022	0,091	0,158
PS_Transport_2	0,073	0,060	0,062	0,029	0,068	0,093

mean Velocity	Males		Females		Subadults	
Phase	mean	SD	mean	SD	mean	SD
FO_Capture	222,434	77,697	236,451	57,521	221,486	91,492
FC_Capture	270,736	104,717	284,675	115,671	291,211	101,857
PS_Capture	40,283	35,725	53,092	38,237	38,519	29,667
SO_Manipulation_1	13,093	8,490	16,892	18,007	24,669	23,018
FO_Manipulation_1	190,317	71,007	159,831	75,011	174,860	72,763
FC_Manipulation_1	240,930	90,970	197,052	77,427	206,004	91,100
PS_Manipulation_1	34,497	39,345	30,784	19,613	39,650	35,004
SO_Manipulation_2	9,757	6,252	9,859	6,131	23,881	20,062
FO_Manipulation_2	125,979	25,017	125,723	55,833	136,800	54,755
FC_Manipulation_2	121,626	36,542	148,816	77,525	155,572	73,543
PS_Manipulation_2	24,099	11,969	29,310	22,451	29,484	31,227
SO_Transport_1	10,516	5,439	16,609	19,049	23,748	26,551
FO_Transport_1	151,927	42,147	155,031	84,407	173,976	72,825
FC_Transport_1	153,712	67,669	174,409	80,323	194,972	74,370
PS_Transport_1	25,164	15,070	37,027	36,912	43,141	37,644
SO_Transport_2	13,667	12,503	9,875	5,268	13,203	7,843
FO_Transport_2	112,151	39,048	99,342	50,905	111,837	45,581
FC_Transport_2	100,015	37,985	106,195	58,092	102,541	39,099
PS_Transport_2	27,138	14,783	27,754	17,052	36,843	20,198

max. Velocity (5)	Males		Females		Subadults	
Phase	mean	SD	mean	SD	mean	SD
FO_Capture	390,511	106,619	378,409	81,747	402,850	98,630
FC_Capture	537,865	181,495	522,913	149,311	523,690	90,325
PS_Capture	161,799	80,223	149,523	65,624	138,818	64,654
SO_Manipulation_1	55,762	37,186	63,859	36,819	64,114	41,771
FO_Manipulation_1	310,689	104,281	235,071	87,791	238,465	78,202
FC_Manipulation_1	371,315	103,699	299,694	98,262	280,850	85,559
PS_Manipulation_1	107,069	40,967	103,094	44,417	117,696	55,542
SO_Manipulation_2	42,535	16,149	52,191	22,101	69,511	48,155
FO_Manipulation_2	221,423	39,760	213,456	73,147	214,971	61,524
FC_Manipulation_2	224,585	64,036	257,047	93,882	244,405	75,982
PS_Manipulation_2	77,887	38,790	84,240	44,206	107,228	40,906
SO_Transport_1	52,016	29,236	70,116	30,351	58,989	36,861
FO_Transport_1	272,290	68,847	226,906	95,390	269,197	90,655
FC_Transport_1	259,284	85,753	277,345	94,656	289,849	89,395
PS_Transport_1	90,350	51,270	107,874	44,841	109,520	50,534
SO_Transport_2	51,552	12,503	58,747	24,324	53,615	33,547
FO_Transport_2	210,460	60,409	185,166	71,516	187,905	57,463
FC_Transport_2	181,810	66,674	190,927	76,393	174,352	66,504
PS_Transport_2	78,634	46,200	83,988	36,317	91,435	42,871

The mean duration of the capture cycle is the shortest compared to the other cycles. It is important to note, that this is the only cycle where only three, instead of four, phases are present (SO is missing). The adult males show always a longer mean duration time than the adult females. In the manipulation_2, transport_1 and transport_2 cycle the adult males and adult females show a longer mean duration time than the subadults. In the capture and the manipulation_1 cycle the subadults show the longest mean duration (see table 6).

Table 6 Mean duration of the five gape cycles of Eublepharis macularius *during the consumption of* Acheta domesticus *(duration in s). (N=10)*

Gape cycle	Males		Females		Subadults	
Capture	0,156	0,068	0,128	0,063	0,166	0,080
Manipulation_1	0,272	0,113	0,257	0,129	0,315	0,524
Manipulation_2	0,363	0,138	0,329	0,125	0,223	0,084
Transport_1	0,374	0,139	0,326	0,196	0,299	0,503
Transport_2	0,398	0,152	0,364	0,145	0,362	0,423

Duration, mean velocity and max velocity – Galleriinae

The SO phases in all cycles shows the longest mean duration time in all three groups (males, females and subadults). The PS phase shows the second longest mean duration time, whereas FO and FC in all cycles (except the capture cycle) show similar means, the similarity is also between the three groups. The adult females show the longest mean duration in all SO and PS phases compared to the adult males and subadults. The fastest phases comparing the mean velocity are in all groups again the FO and the FC phase, but they decrease with the ongoing feeding cycle. In all three groups the second cycles (manipulation_2 and transport_2) are slower in the FO and FC phase compared to their previous cycles. The adult males show in all cycle faster phases than the adult females. With two exceptions, capture (FC) and transport_1 (PS), they are also faster than the subadults. The subadults on the other hand show also higher mean velocities in the whole transport_2 cycle than the adult females. Also in the mean of the max. vel. (5) the SO and the PS phase are always the slowest compared to the FO and FC phase. The FC is in all cycles of the males the fastest phase. The adult females performed in the capture and the transport_2 cycle the slowest max. vel. (5). The adult males show in all phases of all cycles a faster max. vel. (5) than the subadults (see table 7).

Table 7 Duration (s), mean velocity (mm/s) and max velocity (mm/s) of all phases of the feeding cycle of Eublepharis macularius*. Consumption of* Galleriinae*. (N=8)*

Duration	**Males**		**Females**		**Subadults**	
Phase	mean	SD	mean	SD	mean	SD
FO_Capture	0,076	0,040	0,095	0,040	0,075	0,028
FC_Capture	0,067	0,041	0,073	0,041	0,051	0,026
PS_Capture	0,051	0,052	0,162	0,052	0,092	0,049
SO_Manipulation_1	0,094	0,040	0,189	0,040	0,103	0,063
FO_Manipulation_1	0,029	0,008	0,030	0,008	0,029	0,010
FC_Manipulation_1	0,031	0,009	0,042	0,009	0,038	0,022
PS_Manipulation_1	0,050	0,023	0,102	0,023	0,087	0,043
SO_Manipulation_2	0,111	0,043	0,227	0,043	0,113	0,024
FO_Manipulation_2	0,040	0,010	0,035	0,010	0,038	0,013
FC_Manipulation_2	0,037	0,009	0,051	0,009	0,049	0,017
PS_Manipulation_2	0,072	0,030	0,083	0,030	0,083	0,042
SO_Transport_1	0,151	0,054	0,200	0,054	0,114	0,041
FO_Transport_1	0,031	0,014	0,044	0,014	0,037	0,007
FC_Transport_1	0,047	0,030	0,044	0,030	0,050	0,011
PS_Transport_1	0,064	0,029	0,085	0,029	0,066	0,033
SO_Transport_2	0,139	0,052	0,169	0,052	0,118	0,030
FO_Transport_2	0,031	0,006	0,045	0,006	0,054	0,026
FC_Transport_2	0,037	0,010	0,058	0,010	0,051	0,007
PS_Transport_2	0,053	0,021	0,082	0,021	0,046	0,018

mean Velocity	Males		Females		Subadults	
Phase	mean	SD	mean	SD	mean	SD
FO_Capture	194,500	97,844	122,821	65,700	150,243	61,226
FC_Capture	168,882	48,106	116,088	59,475	202,547	62,160
PS_Capture	56,115	39,269	13,695	17,302	26,170	26,876
SO_Manipulation_1	24,673	10,483	13,236	5,705	21,142	20,104
FO_Manipulation_1	164,455	82,526	152,381	63,066	147,018	39,606
FC_Manipulation_1	184,248	71,776	131,914	61,644	167,002	74,713
PS_Manipulation_1	45,735	15,410	24,350	16,222	16,846	8,954
SO_Manipulation_2	18,627	10,026	13,163	7,668	9,432	2,662
FO_Manipulation_2	129,533	55,349	117,890	70,088	105,300	32,536
FC_Manipulation_2	159,116	46,053	100,760	53,977	100,373	33,953
PS_Manipulation_2	31,667	10,782	25,852	6,494	15,547	5,786
SO_Transport_1	16,153	8,839	11,163	2,843	9,777	6,728
FO_Transport_1	174,971	113,320	111,055	40,683	114,913	25,060
FC_Transport_1	196,148	129,095	120,049	30,017	112,677	44,850
PS_Transport_1	26,994	13,727	24,844	6,517	29,369	15,893
SO_Transport_2	20,553	5,487	10,950	5,014	12,917	3,405
FO_Transport_2	106,660	34,734	81,957	33,097	92,495	34,574
FC_Transport_2	139,384	38,011	75,722	20,375	102,300	35,027
PS_Transport_2	52,818	30,410	25,465	9,368	45,950	22,265

max. Velocity (5)	Males		Females		Subadults	
Phase	**mean**	**SD**	**mean**	**SD**	**mean**	**SD**
FO_Capture	337,038	138,124	240,547	95,941	319,029	141,165
FC_Capture	500,651	161,041	381,196	177,010	496,596	105,543
PS_Capture	149,071	48,521	101,941	34,782	105,420	29,682
SO_Manipulation_1	65,929	25,556	62,064	24,281	63,249	27,159
FO_Manipulation_1	222,950	108,493	220,581	87,525	220,518	46,971
FC_Manipulation_1	267,219	86,713	233,250	120,241	267,287	77,069
PS_Manipulation_1	113,123	48,722	113,447	35,417	83,697	34,859
SO_Manipulation_2	67,025	21,446	56,952	24,330	42,455	17,149
FO_Manipulation_2	212,490	107,075	163,084	84,390	163,934	32,438
FC_Manipulation_2	253,145	54,901	184,248	93,928	176,892	24,181
PS_Manipulation_2	100,293	35,155	78,677	19,588	71,334	22,368
SO_Transport_1	56,300	23,646	57,939	25,408	31,411	15,028
FO_Transport_1	251,346	144,614	201,347	53,027	199,611	52,200
FC_Transport_1	310,835	131,199	199,715	46,783	215,643	62,882
PS_Transport_1	86,879	43,627	80,762	22,198	77,075	31,238
SO_Transport_2	63,516	23,944	39,970	14,405	54,833	27,817
FO_Transport_2	147,359	42,291	136,573	43,050	158,945	43,053
FC_Transport_2	208,570	52,147	133,220	31,618	134,468	119,254
PS_Transport_2	118,522	52,022	69,703	21,113	86,202	8,862

The duration of all cycles of the adult females show similar means. And at the same time, the females show the longest mean duration in all cycles compared to the ones of the adult males and subadults. The adult males show the fastest capture cycle and similar means in the other cycles than the subadults (see table 8).

Table 8 Mean duration of the five gape cycles of Eublepharis macularius *during the consumption of Gallerinae (duration in s). (N=8)*

Gape cycle	Males		Females		Subadults	
Capture	0,194	0,056	0,330	0,141	0,209	0,046
Manipulation_1	0,204	0,067	0,363	0,106	0,258	0,094
Manipulation_2	0,260	0,052	0,395	0,128	0,282	0,053
Transport_1	0,293	0,062	0,372	0,100	0,267	0,041
Transport_2	0,259	0,053	0,353	0,102	0,269	0,043

Statistical Analysis – duration, mean velocities and max. vel. (5)

Comparing the durations, mean velocities and max. vel. (5) during the food intake of *Acheta domesticus*, there were no significant differences between the three groups in the capture phase. Whereas in the manipulation_1 cycle the males show in some phases higher max. vel. (5) than the females and subadults. In the two transport cycles the males on the other hand show the longest duration time. In the slow opening phase of the manipulation_2 cycle the subadults show, with high significance, faster velocities than the males and females. For more detail see table 9.

Table 9 Statistical analysis of duration, mean velocity and max. vel. (5) of Eublepharis macularius during the food intake of Acheta domesticus. *(*) p value < 0,05; (**) p value < 0,01. (one-way ANOVA analysis and if significant a pairwise analysis by the Bonferroni post hoc test*

FO_Capture	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Duration	F = 2,12, p = 0,13	H_0 is not rejected
Mean_Velocity	F = 0,22, p = 0,801	H_0 is not rejected
max_Velocity (5)	F = 0,29, p = 0,748	H_0 is not rejected

FC_Capture	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Duration	F = 0,48, p = 0,62	H_0 is not rejected
Mean_Velocity	F = 0,17, p = 0,847	H_0 is not rejected
max_Velocity (5)	F = 0,06, p = 0,942	H_0 is not rejected

PS_Capture	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Duration	F = 1,94, p = 0,153	H_0 is not rejected
Mean_Velocity	F = 0,96, p = 0,391	H_0 is not rejected
max_Velocity (5)	F = 0,45, p = 0,639	H_0 is not rejected

SO_Man_1	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Duration	F = 0,1, p = 0,903	H_0 is not rejected
Mean_Velocity	F = 2,03, p = 0,141	H_0 is not rejected
max_Velocity (5)	F = 0,27, p = 0,761	H_0 is not rejected

FO_Man_1	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Duration	F = 1,02, p = 0,368	H_0 is not rejected
Mean_Velocity	F = 0,81, p = 0,452	H_0 is not rejected
max_Velocity (5)	F = 4,04, p = 0,023*	males > females *

FC_Man_1	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Duration	F = 0,78, p = 0,462	H_0 is not rejected
Mean_Velocity	F = 1,31, p = 0,278	H_0 is not rejected
max_Velocity (5)	F = 4,45, p = 0,016*	males > subadults*

PS_Man_1	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Duration	gibt F = 0,66, p = 0,522	H_0 is not rejected
Mean_Velocity	F = 0,35, p = 0,706	H_0 is not rejected
max_Velocity (5)	F = 0,46, p = 0,632	H_0 is not rejected

SO_Man_2	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Duration	F = 6,75, p = 0,002**	males > females ** females > subadults**
Mean_Velocity	F = 7,45, p = 0,001**	subadults > males ** subadults > females**
max_Velocity (5)	F = 3,26, p = 0,046	subadults > males*

FO_Man_2	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Duration	F = 2,4, p = 0,1	H_0 is not rejected
Mean_Velocity	F = 0,3, p = 0,742	H_0 is not rejected
max_Velocity (5)	F = 0,09, p = 0,914	H_0 is not rejected

FC_Man_2	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Duration	F = 0,83, p = 0,442	H_0 is not rejected
Mean_Velocity	F = 1,33, p = 0,273	H_0 is not rejected
max_Velocity (5)	F = 0,78, p = 0,463	H_0 is not rejected

PS_Man_2	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Duration	F = 1,71, p = 0,19	H_0 is not rejected
Mean_Velocity	F = 2,23, p = 0,118	H_0 is not rejected
max_Velocity (5)	F = 2,23, p = 0,117	H_0 is not rejected

SO_TP_1	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Duration	F = 5,83, p = 0,005**	males > subadults ** females > subadults *
Mean_Velocity	F = 2,16, p = 0,125	H0 is not rejected
max_Velocity (5)	F = 1,48, p = 0,236	H_0 is not rejected

FO_TP_1	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Duration	F = 3,54, p = 0,036*	males > subadults*
Mean_Velocity	F = 0,54, p = 0,586	H_0 is not rejected
max_Velocity (5)	F = 1,62, p = 0,207	H_0 is not rejected

FC_TP_1	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Duration	F = 6,44, p = 0,003**	males > females* males > subadults **
Mean_Velocity	F = 1,38, p = 0,259	H_0 is not rejected
max_Velocity (5)	F = 0,52, p = 0,595	H_0 is not rejected

PS_TP_1	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Duration	F = 3,45, p = 0,039*	males > subadults *
Mean_Velocity	F = 0,99, p = 0,377	H_0 is not rejected
max_Velocity (5)	F = 0,85, p = 0,434	H_0 is not rejected

SO_TP_2	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Duration	F = 1,73, p = 0,186	H_0 is not rejected
Mean_Velocity	F = 1,38, p = 0,261	H_0 is not rejected
max_Velocity (5)	F = 0,36, p = 0,699	H_0 is not rejected

FO_TP_2	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Duration	F = 0,97, p = 0,386	H_0 is not rejected
Mean_Velocity	F = 0,48, p = 0,621	H_0 is not rejected
max_Velocity (5)	F = 0,87, p = 0,425	H_0 is not rejected

FC_TP_2	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Duration	F = 3,25, p = 0,046*	males > subadults*
Mean_Velocity	F = 0,08, p = 0,92	H_0 is not rejected
max_Velocity (5)	F = 0,26, p = 0,772	H_0 is not rejected

PS_TP_2	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Duration	F = 1,14, p = 0,328	H_0 is not rejected
Mean_Velocity	F = 1,75, p = 0,183	H_0 is not rejected
max_Velocity (5)	F = 0,42, p = 0,656	H_0 is not rejected

Comparing the duration, mean velocities and the max. vel. (5) of all three groups during the food intake of *Galleriinae*, in most cycles there were no significant differences detected. In the significant phases the Bonferroni post hoc pairwise analysis showed, with one exceptions, that the males had the highest mean velocity. For more detail see table 10.

Table 10 Statistical analysis of duration, mean velocity and max. vel. (5) of Eublepharis macularius during the food intake of Galleriinae*. (*) p value < 0,05; (**) p value < 0,01. (one-way ANOVA analysis and if significant a pairwise analysis by the Bonferroni post hoc test.*

FO_Capture	**one-way analysis of variance (one-way ANOVA)**	**post hoc analysis (Bonferroni)**
Duration	F = 0,66, p = 0,528	H_0 is not rejected
Mean_Velocity	F = 1,56, p = 0,234	H_0 is not rejected
max_Velocity (5)	F = 1,15, p = 0,337.	H_0 is not rejected

FC_Capture	**one-way analysis of variance (one-way ANOVA)**	**post hoc analysis (Bonferroni)**
Duration	F = 0,59, p = 0,564	H_0 is not rejected
Mean_Velocity	F = 3,89, p = 0,037*	subadults > females *
max_Velocity (5)	F = 1,35, p = 0,283	H_0 is not rejected

PS_Capture	**one-way analysis of variance (one-way ANOVA)**	**post hoc analysis (Bonferroni)**
Duration	F = 2,65, p = 0,095	H_0 is not rejected
Mean_Velocity	F = 3,83, p = 0,039*	males > females *
max_Velocity (5)	F = 2,79, p = 0,088	H_0 is not rejected

SO_Man_1	**one-way analysis of variance (one-way ANOVA)**	**post hoc analysis (Bonferroni)**
Duration	F = 3,45, p = 0,052	H_0 is not rejected
Mean_Velocity	F = 1,38, p = 0,275	H_0 is not rejected
max_Velocity (5)	F = 0,04, p = 0,96	H_0 is not rejected

FO_Man_1	**one-way analysis of variance (one-way ANOVA)**	**post hoc analysis (Bonferroni)**
Duration	F = 0,02, p = 0,979	H_0 is not rejected
Mean_Velocity	F = 0,12, p = 0,883	H_0 is not rejected
max_Velocity (5)	F = 0, p = 0,998	H_0 is not rejected

FC_Man_1	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Duration	F = 0,95, p = 0,405	H_0 is not rejected
Mean_Velocity	F = 1,02, p = 0,377	H_0 is not rejected
max_Velocity (5)	F = 0,28, p = 0,761	H_0 is not rejected

PS_Man_1	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Duration	*F* = 3,67, *p* = 0,044*	females > males *
Mean_Velocity	*F* = 7,54, *p* = 0,004**	males > females * females > subadults *
max_Velocity (5)	*F* = 1,14, *p* = 0,341.	H_0 is not rejected

SO_Man_2	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Duration	*F* = 6,05, *p* = 0,009**	females > males * females > subadults *
Mean_Velocity	*F* = 2,44, *p* = 0,113	H_0 is not rejected
max_Velocity (5)	*F* = 2,16, *p* = 0,141	H_0 is not rejected

FC_Man_1	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Duration	*F* = 0,25, *p* = 0,778	H_0 is not rejected
Mean_Velocity	*F* = 0,31, *p* = 0,738	H_0 is not rejected
max_Velocity (5)	*F* = 0,8, *p* = 0,462	H_0 is not rejected

FC_Man_2	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Duration	*F* = 2,5, *p* = 0,107	H_0 is not rejected
Mean_Velocity	*F* = 3,7, *p* = 0,043*	males > females * males > subadults *
max_Velocity (5)	*F* = 2,78, *p* = 0,086	H_0 is not rejected

PS_Man_2	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Duration	*F* = 0,23, *p* = 0,797	H_0 is not rejected
Mean_Velocity	*F* = 6,56, *p* = 0,006**	males > females * males > subadults*
max_Velocity (5)	*F* = 2,11, *p* = 0,147	H_0 is not rejected

SO_TP_1	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Duration	F = 2,91, p = 0,078	H_0 is not rejected
Mean_Velocity	F = 1,72, p = 0,205	H_0 is not rejected
max_Velocity (5)	F = 2,88, p = 0,08	H_0 is not rejected

FO_TP_1	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Duration	F = 1,12, p = 0,346	H_0 is not rejected
Mean_Velocity	F = 1,68, p = 0,212	H_0 is not rejected
max_Velocity (5)	F = 0,65, p = 0,535	H_0 is not rejected

FC_TP_1	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Duration	F = 0,13, p = 0,883	H_0 is not rejected
Mean_Velocity	F = 2,15, p = 0,143	H_0 is not rejected
max_Velocity (5)	F = 3,12, p = 0,066	H_0 is not rejected

PS_TP_1	one-way analysis of variance (one-way ANOVA)	post hoc analysis(Bonferroni)
Duration	F = 1,11, p = 0,349	H_0 is not rejected
Mean_Velocity	F = 0,21, p = 0,811	H_0 is not rejected
max_Velocity (5)	F = 0,14, p = 0,868	H_0 is not rejected

SO_TP_2	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Duration	F = 0,78, p = 0,472	H_0 is not rejected
Mean_Velocity	F = 7,8, p = 0,003**	males > females * males > subadults *
max_Velocity (5)	F = 1,94, p = 0,17	H_0 is not rejected

FO_TP_2	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Duration	F = 2,87, p = 0,08	H_0 is not rejected
Mean_Velocity	F = 0,92, p = 0,416	H_0 is not rejected
max_Velocity (5)	F = 0,44, p = 0,648	H_0 is not rejected

FC_TP_2	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Duration	F = 5,14, p = 0,016*	males > females *
Mean_Velocity	F = 6,97, p = 0,005**	males > females *
max_Velocity (5)	F = 2,26, p = 0,131	H_0 is not rejected

FO_TP_2	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Duration	F = 2,95, p = 0,075	H_0 is not rejected
Mean_Velocity	F = 2,78, p = 0,086	H_0 is not rejected
max_Velocity (5)	F = 3,82, p = 0,039*	males > females*

*Duration, mean velocity and max velocity – statistical analysis comparing the two different feeds (*Acheta domesticus *&.* Galleriinae)

The following description sums up the significant, and therefore, the important phases of the three individual groups (males, females and subadults) while comparing them between the two different prey items (*Acheta domesticus* and *Galleriinae*).

Comparing the two different feeds in males:

In the FC phase of the capture cycle the Levene test of equality of variance yields a p-value of 0.092, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. Thus, there is equality of variance in the samples. A two-tailed t-test for independent samples (equal variances assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable "duration" was statistically significant, t(25) = -2.19, p = 0.038, 95% confidence interval [-0.05, -0]. The h_0 is thus rejected. (*Galleriinae* > *Acheta domesticus*)

The Levene test of equality of variance yields a p-value of 0.036, which is below the 5% significance level. The Levene test is therefore significant and the h_0 that all variances of the groups are equal is rejected. A two-tailed t-test for independent samples (equal variances not assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable "mean Velocity" was statistically significant, t(24,38) = 3.32, p = 0.003, 95% confidence interval [38.63, 165.08]. The h_0 is thus rejected. (*Acheta domesticus* > *Galleriinae*)

In the SO phase of the manipulation_1 cycle the Levene test of equality of variance yields a p-value of 0.244, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. A two-tailed t-test for independent samples

(equal variances assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable “mean Velocity” was statistically significant, t(25) = -2.9, p = 0.008, 95% confidence interval [-19.81, -3.35]. The h_0 is thus rejected. (*Galleriinae* > *Acheta domesticus*)

In the FO phase the Levene test of equality of variance yields a p-value of 0.466, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. A two-tailed t-test for independent samples (equal variances assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable “max. vel. (5)” was statistically significant, t(25) = 2.33, p = 0.028, 95% confidence interval [11.78, 188.7]. The h_0 is thus rejected. (*Acheta domesticus* > *Galleriinae*)

In the FC phase the Levene test of equality of variance yields a p-value of 0.399, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. A two-tailed t-test for independent samples (equal variances assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable “max. vel. (5)” was statistically significant, t(25) = 2.4, p = 0.024, 95% confidence interval [14.8, 193.4]. The h_0 is thus rejected. (*Acheta domesticus* > *Galleriinae*)

In the PS phase the Levene test of equality of variance yields a p-value of 0.053, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. A two-tailed t-test for independent samples (equal variances assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable “mean Velocity” was statistically significant, t(24) = -4.3, p = <0.001, 95% confidence interval [-30.84, -10.83]. The h_0 is thus rejected. (*Acheta domesticus* > *Galleriinae*)

In the SO phase of the manipulation_2 cycle the Levene test of equality of variance yields a p-value of 0.015, which is below the significance level of 5%. The Levene test is therefore significant and the h_0 that all variances of the groups are equal is rejected. A two-tailed t-test for independent samples (equal variances not assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable “mean Velocity” was statistically significant, t(7,91) = -2.57, p = 0.034, 95% confidence interval [-19.07, -1]. The h_0 is thus rejected. (*Acheta domesticus* > *Galleriinae*)

The Levene test of equality of variance yields a p-value of 0.12, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. A two-tailed t-test for independent samples (equal variances assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable “max.

vel. (5)" was statistically significant, t(25) = -3.13, p = 0.004, 95% confidence interval [-40.62, -8.35]. The h_0 is thus rejected. (*Acheta domesticus* > *Galleriinae*)

In the FC phase the Levene test of equality of variance yields a p-value of 0.719, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. A two-tailed t-test for independent samples (equal variances assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable "mean Velocity" was statistically significant, t(25) = -2.16, p = 0.04, 95% confidence interval [-73.22, -1.76]. The h_0 is thus rejected. (*Acheta domesticus* > *Galleriinae*)

In the PS phase the Levene test of equality of variance yields a p-value of 0.455, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. A two-tailed t-test for independent samples (equal variances assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable "mean Velocity" was statistically significant, t(24) = -2.15, p = 0.042, 95% confidence interval [-18.38, -0.38]. The h_0 is thus rejected. (*Acheta domesticus* > *Galleriinae*)

In the SO phase of the transport_1 cycle the Levene test of equality of variance yields a p-value of 0.854, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. A two-tailed t-test for independent samples (equal variances assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable "mean Velocity" was statistically significant, t(24) = -3.93, p = 0.001, 95% confidence interval [-14.57, -4.53]. The h_0 is thus rejected. (*Galleriinae* > *Acheta domesticus*)

In the FO phase of the Levene test of equality of variance yields a p-value of 0.042, which is below the 5% significance level. The Levene test is therefore significant and the h_0 that all variances of the groups are equal is rejected. A two-tailed t-test for independent samples (equal variances not assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable "duration" was statistically significant, t(23,24) = 3.42, p = 0.002, 95% confidence interval [0.01, 0.03]. The h_0 is thus rejected. (*Acheta domesticus* > *Galleriinae*)

The Levene test of equality of variance yields a p-value of 0.392, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. A two-tailed t-test for independent samples (equal variances assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable "max.

vel. (5)" was statistically significant, t(25) = 2.59, p = 0.016, 95% confidence interval [12.88, 113.32]. The h_0 is thus rejected. (*Acheta domesticus* > *Galleriinae*)

In the FC phase of the Levene test of equality of variance yields a p-value of 0.021, which is below the 5% significance level. The Levene test is therefore significant and the h_0 that all variances of the groups are equal is rejected. A two-tailed t-test for independent samples (equal variances not assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable "duration" was statistically significant, t(24,18) = 4.32, p = <0.001, 95% confidence interval [0.02, 0.06]. The h_0 is thus rejected. (*Acheta domesticus* > *Galleriinae*)

The Levene test of equality of variance yields a p-value of 0.732, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. A two-tailed t-test for independent samples (equal variances assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable "mean Velocity" was statistically significant, t(25) = -2.37, p = 0.026, 95% confidence interval [-73.65, -5.09]. The h_0 is thus rejected. (*Galleriinae* > *Acheta domesticus*)

In the PS phase of the Levene test of equality of variance yields a p-value of <0.001, which is below the 5% significance level. The Levene test is therefore significant and the h_0 that all variances of the groups are equal is rejected. A two-tailed t-test for independent samples (equal variances not assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable "mean Velocity" was statistically significant, t(7,86) = -2.45, p = 0.041, 95% confidence interval [-56.37, -1.59]. The h_0 is thus rejected. (*Galleriinae* > *Acheta domesticus*)

The Levene test of equality of variance yields a p-value of 0.514, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. A two-tailed t-test for independent samples (equal variances assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable "max. vel. (5)" was statistically significant, t(24) = -2.41, p = 0.024, 95% confidence interval [-85.71, -6.56]. The h_0 is thus rejected. (*Galleriinae* > *Acheta domesticus*)

Comparing the two different feeds in females:

In the FO phase of the capture cycle the Levene test of equality of variance yields a p-value of 0.002, which is below the significance level of 5%. The Levene test is therefore significant and the h_0 that all variances of the groups are equal is rejected. A two-tailed t-test for independent samples (equal variances not assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with

respect to the dependent variable “duration” was statistically significant, t(7,34) = -3.21, p = 0.014, 95% confidence interval [-0.08, -0.01]. The h_0 is thus rejected. (*Galleriinae* > *Acheta domesticus*)

The Levene test of equality of variance yields a p-value of 0.555, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. A two-tailed t-test for independent samples (equal variances assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable “mean Velocity” was statistically significant, t(25) = 4.21, p = <0.001, 95% confidence interval [57.34, 167.15]. The h_0 is thus rejected. (*Acheta domesticus* > *Galleriinae*)

The Levene test of equality of variance yields a p-value of 0.324, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. A two-tailed t-test for independent samples (equal variances assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable “max. vel. (5)” was statistically significant, t(25) = 3.66, p = 0.001, 95% confidence interval [61.28, 218.73]. The h_0 is thus rejected. (*Acheta domesticus* > *Galleriinae*)

In the FC phase of the Levene test of equality of variance yields a p-value of 0.062, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. A two-tailed t-test for independent samples (equal variances assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable “mean Velocity” was statistically significant, t(25) = 3.66, p = 0.001, 95% confidence interval [73.17, 261.96]. The h_0 is thus rejected. (*Acheta domesticus* > *Galleriinae*)

The Levene test of equality of variance yields a p-value of 0.272, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. A two-tailed t-test for independent samples (equal variances assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable “max. vel. (5)” was statistically significant, t(22) = 2.9, p = 0.008, 95% confidence interval [53.36, 321.05]. The h_0 is thus rejected. (*Acheta domesticus* > *Galleriinae*)

In the PS phase of the Levene test of equality of variance yields a p-value of 0.003, which is below the significance level of 5%. The Levene test is therefore significant and the h_0 that all variances of the groups are equal is rejected. A two-tailed t-test for independent samples (equal variances not assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable “duration” was statistically significant, t(7,45) = -2.51, p = 0.039, 95% confidence interval [-0.25, -0.01]. The h_0 is thus rejected. (*Galleriinae* > *Acheta domesticus*)

The Levene test of equality of variance yields a p-value of 0.066, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. A two-tailed t-test for independent samples (equal variances assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable "mean Velocity" was statistically significant, t(25) = 2.63, p = 0.014, 95% confidence interval [8.5, 70.27]. The h_0 is thus rejected. (*Acheta domesticus* > *Galleriinae*)

In the PS phase of the manipulation_1 cycle the Levene test of equality of variance yields a p-value of 0.697, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. A two-tailed t-test for independent samples (equal variances assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable "duration" was statistically significant, t(25) = -2.31, p = 0.029, 95% confidence interval [-0.08, -0]. The h_0 is thus rejected. (*Galleriinae* > *Acheta domesticus*)

In the FO phase of the manipulation_2 cycleThe Levene test of equality of variance yields a p-value of 0.456, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. A two-tailed t-test for independent samples (equal variances assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable "max. vel. (5")" was statistically significant, t(24) = 2.16, p = 0.041, 95% confidence interval [3.25, 141.07]. The h_0 is thus rejected. (*Acheta domesticus* > *Galleriinae*)

In the FC phase of the transport_1 cycle the Levene test of equality of variance yields a p-value of 0.098, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. A two-tailed t-test for independent samples (equal variances assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable "mean Velocity" was statistically significant, t(24) = 2.12, p = 0.045, 95% confidence interval [1.05, 80.49]. The h_0 is thus rejected. (*Acheta domesticus* > *Galleriinae*)

The Levene test of equality of variance yields a p-value of 0.188, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. A two-tailed t-test for independent samples (equal variances assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable "max. vel. (5)" was statistically significant, t(24) = 2.28, p = 0.032, 95% confidence interval [6.29, 125.67]. The h_0 is thus rejected. (*Acheta domesticus* > *Galleriinae*)

In the FC phase of the transport_2 cycle the Levene test of equality of variance yields a p-value of 0.016, which is below the significance level of 5%. The Levene test is therefore significant and the h_0 that all variances of the groups are equal is rejected. A two-tailed t-test for independent samples (equal variances not assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable "max. vel. (5)" was statistically significant, t(23,13) = 3.23, p = 0.004, 95% confidence interval [23.09, 105.47]. The h_0 is thus rejected. (*Acheta domesticus* > *Galleriinae*)

Comparing the two different feeds in subadults:

In the FO-Capture phase the results of the Levene test of variance equality, for the dependent variable "max. vel. (5)", yields a p-value of 0.122, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. The two-tailed t-test for independent samples (equal variances assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable "max. vel. (5)" was statistically significant, t(24) = 3.41, p = 0.002, 95% confidence interval [52.88, 214.76]. The h_0 is thus rejected. (*Acheta domesticus* > *Galleriinae*)

In the SO_Man_2 phase the results of the Levene test of variance equality, for the dependent variable "duration", yields a p-value of 0.084, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. The two-tailed t-test for independent samples (equal variances assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable "duration" was statistically significant, t(22) = -2.56, p = 0.018, 95% confidence interval [-0.08, -0.01]. The h_0 is thus rejected. (*Galleriinae* > *Acheta domesticus*)

In the FC_Man_2 phase the results of the Levene test of variance equality, for the dependent variable "duration", yields a p-value of 0.139, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. The two-tailed t-test for independent samples (equal variances assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable "duration" was statistically significant, t(22) = -2.21, p = 0.037, 95% confidence interval [-0.03, -0]. The h_0 is thus rejected. (*Galleriinae* > *Acheta domesticus*)

In the FC_Man_2 phase the results of the Levene test of variance equality, for the dependent variable "mean velocity", yields a p-value of 0.007, which is below the significance level of 5%. The Levene test is therefore significant and the h_0 that all variances of the groups are equal is rejected. The two-tailed t-test for independent samples (equal variances not assumed) showed that the difference between

Acheta domesticus and *Galleriinae* with respect to the dependent variable “mean Velocity” was statistically significant, t(17,49) = 3.69, p = 0.002, 95% confidence interval [29.84, 109.13]. The h_0 is thus rejected. (*Acheta domesticus* > *Galleriinae*)

In the FC_Man_2 phase the results of the Levene test of variance equality, for the dependent variable “max. vel. (5)”, yields a p-value of 0.007, which is below the significance level of 5%. The Levene test is therefore significant and the h_0 that all variances of the groups are equal is rejected. The two-tailed t-test for independent samples (equal variances not assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable “max. vel. (5)” was statistically significant, t(21,61) = 3.15, p = 0.005, 95% confidence interval [23.06, 111.96]. The h_0 is thus rejected. (*Acheta domesticus* > *Galleriinae*)

In the PS_Man_2 phase the results of the Levene test of variance equality, for the dependent variable “mean velocity”, yields a p-value of 0.034, which is below the significance level of 5%. The Levene test is therefore significant and the h_0 that all variances of the groups are equal is rejected. The two-tailed t-test for independent samples (equal variances not assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable “mean Velocity” was statistically significant, t(20,98) = 3.92, p = 0.001, 95% confidence interval [10.39, 33.93]. The h_0 is thus rejected. (*Acheta domesticus* > *Galleriinae*)

In the PS_Man_2 phase the results of the Levene test of variance equality, for the dependent variable “max. vel. (5)”, yields a p-value of 0.045, which is below the significance level of 5%. The Levene test is therefore significant and the h_0 that all variances of the groups are equal is rejected. The two-tailed t-test for independent samples (equal variances not assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable “max. vel. (5)” was statistically significant, t(19,11) = 2.57, p = 0.019, 95% confidence interval [6.68, 65.11]. The h_0 is thus rejected. (*Acheta domesticus* > *Galleriinae*)

In the SO_TP_1 phase the results of the Levene test of variance equality, for the dependent variable “mean velocity”, yields a p-value of 0.044, which is below the significance level of 5%. The Levene test is therefore significant and the h_0 that all variances of the groups are equal is rejected. The two-tailed t-test for independent samples (equal variances not assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable “mean Velocity” was statistically significant, t(18,71) = 2.64, p = 0.016, 95% confidence interval [3.44, 29.93]. The h_0 is thus rejected. (*Acheta domesticus* > *Galleriinae*)

In the SO_TP_1 phase the results of the Levene test of variance equality, for the dependent variable "max. vel. (5)", yields a p-value of 0.012, which is below the significance level of 5%. The Levene test is therefore significant and the h_0 that all variances of the groups are equal is rejected. The two-tailed t-test for independent samples (equal variances not assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable "max. vel. (5)" was statistically significant, t(19,76) = 3.74, p = 0.001, 95% confidence interval [14.69, 51.9]. The h_0 is thus rejected. (*Acheta domesticus* > *Galleriinae*)

In the FO_TP_1 results of the Levene test of variance equality, for the dependent variable "mean velocity" yields a p-value of 0.176, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. The two-tailed t-test for independent samples (equal variances assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable "mean Velocity" was statistically significant, t(24) = 2.64, p = 0.014, 95% confidence interval [14.54, 119.38]. The h_0 is thus rejected. (*Acheta domesticus* > *Galleriinae*)

In the FC_TP_1 the results of the Levene test of variance equality, for the dependent variable "duration", yields a p-value of 0.647, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. The two-tailed t-test for independent samples (equal variances assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable "duration" was statistically significant, t(24) = -4.05, p = <0.001, 95% confidence interval [-0.03, -0.01]. The h_0 is thus rejected. (*Galleriinae* > *Acheta domesticus*)

In the FC_TP_1 phase the results of the Levene test of variance equality, for the dependent variable "mean velocity", yields a p-value of 0.32, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. The two-tailed t-test for independent samples (equal variances assumed) showed that the difference between *Acheta domesticus* and *Galleriinae* with respect to the dependent variable "mean Velocity" was statistically significant, t(24) = 2.64, p = 0.014, 95% confidence interval [17.99, 146.6]. The h_0 is thus rejected. (*Acheta domesticus* > *Galleriinae*)

In the FC_TP_1 phase the results of the Levene test of variance equality, for the dependent variable "max. vel. (5)", yields a p-value of 0.767, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. The two-tailed t-test for independent samples (equal variances assumed) showed that the difference between *Acheta*

domesticus and *Galleriinae* with respect to the dependent variable "max. vel. (5)" was statistically significant, t(24) = 2.3, p = 0.03, 95% confidence interval [8.23, 150.71]. The h_0 is thus rejected. (*Acheta domesticus* > *Galleriinae*)

In all other cases, the test for independent samples (both for equal and unequal variances) was not statistically significant and thus the null hypothesis was retained.

Angle measurements

Angle measurements - Acheta domesticus

All three groups show the lowest angle change in the fronto-pariental suture in the baseline-SO and the FC-PS phase of all cycles except the capture cycle. The mean of the subadults angle change in the capture cycle (baseline-max) shows the highest change in the dataset. In all other cycles the females show the highest angle change at the fronto-parietal suture compared to the adult males and subadults in the baseline-SO phase (see table 11).

Table 11 Mesokinetic angle change in male, female and subadult Eublepharis macularius *in capture, manipulation and transport cycles during the consumption of* Acheta domesticus. *(N=10)*

Cycle	**Phase**	**Males**		**Females**		**Subadults**	
Capture		mean	SD	mean	SD	mean	SD
	Baseline-Max	+13,16	±3,98	+13,32	±4,38	+14,17	±2,80
	Max-FC	-9,76	±4,05	-8,46	±2,46	-9,65	±4,68
	FC-PS	-6,97	±3,85	-6,18	±4,17	-11,92	±3,61
Manipulation_1							
	Baseline-SO	+2,52	±3,33	+3,87	±3,38	+3,58	±3,16
	SO-Max	+10,82	±3,73	+8,95	±2,90	+9,80	±3,99
	Max-FC	-8,23	±3,71	-8,43	±3,24	-8,71	±4,33
	FC-PS	-7,04	±3,15	-6,65	±5,10	-7,26	±4,72
Manipulation_2							
	Baseline-SO	+2,67	±2,02	+4,96	±3,58	+2,97	±1,87
	SO-Max	+7,56	±2,17	+9,27	±3,86	+9,38	±3,36
	Max-FC	-8,26	±2,92	-8,95	±4,19	-9,31	±4,05
	FC-PS	-3,57	±1,60	-4,85	±3,93	-7,07	±6,00
Transport_1							
	Baseline-SO	+2,49	±2,24	+5,39	±3,01	+3,01	±1,72
	SO-Max	+7,81	±2,37	+7,67	±2,51	+9,46	±3,25
	Max-FC	-8,16	±3,10	-7,74	±3,66	-8,34	±4,42
	FC-PS	-5,02	±2,72	-5,64	±3,31	-7,20	±4,72
Tranport_2							
	Baseline-SO	+3,29	±1,83	+4,27	±3,45	+3,22	±2,30
	SO-Max	+7,77	±3,80	+6,52	±2,63	+7,40	±2,30
	Max-FC	-8,25	±3,68	-6,78	±3,25	-7,01	±3,07
	FC-PS	-3,52	±1,70	-4,36	±1,88	-4,12	±2,53

The statistical analysis of the mesokinetic angle change, measured at the fronto-parietal-suture during the food consumption of *Acheta domesticus* showed some significant differences between the three groups in the phase "baseline to maximum mouth opening" in the manipulation_2 and transport_1 cycles. The females showed here a significant higher angle change than the subadults and males. Whereas the subadults showed a significant higher angle change in the phase "fast closing to power stroke" in the capture and manipulation_2 cycles (see table 12).

Table 12 Statistical analysis of the mesokinetic angle change during the phases of each cycle in Eublepharis macularius. *(*) p value < 0,05; (**) p value < 0,01. (one-way ANOVA analysis and if significant a pairwise analysis by the Bonferroni pot hoc test).*

Capture	**one-way analysis of variance (one-way ANOVA)**	**post hoc analysis (Bonferroni)**
Baseline_Max	F = 0,36, p = 0,701	H_0 is not rejected
Max_FC	F = 0,67, p = 0,516	H_0 is not rejected
FC_PS	F = 11,29, p = <0,001**	subadults > males * subadults > females **

Manipuation_1	**one-way analysis of variance (one-way ANOVA)**	**post hoc analysis (Bonferroni)**
Baseline_SO	F = 0,89, p = 0,418.	H_0 is not rejected
SO_Max	F = 1,3, p = 0,28	H_0 is not rejected
Max_FC	F = 0,08, p = 0,926	H_0 is not rejected
FC_PS	F = 0,09, p = 0,911	H_0 is not rejected

Manipuation_2	**one-way analysis of variance (one-way ANOVA)**	**post hoc analysis (Bonferroni)**
Baseline_SO	F = 4,11, p = 0,022	females > males *
SO_Max	F = 1,89, p = 0,161	H_0 is not rejected
Max_FC	F = 0,37, p = 0,694	H_0 is not rejected
FC_PS	F = 3,21, p = 0,048.	subadults > males *

Transport_1	**one-way analysis of variance (one-way ANOVA)**	**post hoc analysis (Bonferroni)**
Baseline_SO	F = 7,87, p = 0,001	females > males ** females > subadults *
SO_Max	F = 2,46, p = 0,095	H_0 is not rejected
Max_FC	F = 0,13, p = 0,882	H_0 is not rejected
FC_PS	F = 1,74, p = 0,186	H_0 is not rejected

Transport_2	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Baseline_SO	F = 0,94, p = 0,396	H_0 is not rejected
SO_Max	F = 0,88, p = 0,421	H_0 is not rejected
Max_FC	F = 1,05, p = 0,358	H_0 is not rejected
FC_PS	F = 0,83, p = 0,441	H_0 is not rejected

Angle measurements – Galleriinae

During the food intake of the wax moth larvae *Galleriinae* the subadults show the highest mean angle change at the fronto-parietal suture in the capture cycle (Baseline-FO) compared to the adult groups. They also show the highest angle change in the FC-PS phase of the manipulation_1 cycle. The subadults show, with some exception, always the highest angle changes. On the other hand, the adult females show in mostly all cycles, except the manipulation_1 cycle, the lowest angle change at the fronto-parietal suture (see table 13).

Table 13 Mesokinetic angle change in male, female and subadult Eublepharis macularius *in capture, manipulation and transport cycles during the consumption of* Galleriinae*. (N=8)*

Cycle	**Phase**	**Males**		**Females**		**Subadults**	
Capture		mean	SD	mean	SD	mean	SD
	Baseline-Max	+13,07	±2,80	+11,18	±2,46	+15,37	±0,32
	Max-FC	-11,05	±5,32	-12,20	±6,50	-12,09	±3,89
	FC-PS	-8,36	±6,31	-10,66	±4,95	-15,08	±9,78
Manipulation_1							
	Baseline-SO	+2,34	±2,07	+3,03	±2,98	+3,23	±2,60
	SO-Max	+9,48	±3,75	+9,89	±3,58	+9,69	±3,78
	Max-FC	-9,48	±1,97	-10,28	±3,33	-10,47	±1,72
	FC-PS	-8,71	±6,77	-9,43	±2,51	-13,00	±3,24
Manipulation_2							
	Baseline-SO	+4,37	±3,81	+2,84	±1,73	+5,56	±3,93
	SO-Max	+11,96	±4,81	+7,95	±2,54	+8,93	±3,10
	Max-FC	-11,28	±2,99	-9,98	±3,33	-8,43	±0,83
	FC-PS	-7,96	±3,82	-7,41	±4,07	-9,28	±4,93
Transport_1							
	Baseline-SO	+3,23	±1,69	+2,47	±1,73	+5,36	±2,48
	SO-Max	+9,21	±2,53	+9,51	±3,32	+9,23	±0,97
	Max-FC	-11,14	±3,37	-7,24	±2,12	-6,97	±1,61
	FC-PS	-7,39	±3,33	-6,74	±4,11	-13,98	±6,20
Tranport_2							
	Baseline-SO	+3,20	±2,38	+2,58	±1,29	+5,13	±3,16
	SO-Max	+7,75	±2,63	+7,11	±2,40	+8,17	±5,13
	Max-FC	-8,36	±3,34	-6,16	±2,41	-5,91	±0,72
	FC-PS	-6,13	±2,89	-5,47	±3,26	-2,65	±1,67

The statistical analysis of the mesokinetic angle change, measured at the fronto-parietal-suture during the food consumption of *Galleriinae* showed some significant differences between the three groups. In all testes phases with detected significant differences the Bonferroni post hoc pairwise analysis showed that the subadults had higher angle changes than the males and females (for detail see table 14).

Table 14 Statistical analysis of the mesokinetic angle change during the phases of each cycle in Eublepharis macularius. *(*) p value < 0,05; (**) p value < 0,01. (one-way ANOVA analysis and if significant a pairwise analysis by the Bonferroni pot hoc test).*

Capture	**one-way analysis of variance (one-way ANOVA)**	**post hoc analysis (Bonferroni)**
Baseline_Max	F = 5,58, p = 0,012	subadults > females *
Max_FC	F = 0,09, p = 0,913	H_0 is not rejected
FC_PS	F = 5,3, p = 0,014	subadults > males * subadults > females *

Manipuation_1	**one-way analysis of variance (one-way ANOVA)**	**post hoc analysis (Bonferroni)**
Baseline_SO	F = 0,17, p = 0,842	H_0 is not rejected
SO_Max	F = 0,1, p = 0,909	H_0 is not rejected
Max_FC	F = 1,99, p = 0,163	H_0 is not rejected
FC_PS	F = 9,21, p = 0,001	subadults > males *

Manipuation_2	**one-way analysis of variance (one-way ANOVA)**	**post hoc analysis (Bonferroni)**
Baseline_SO	F = 1,51, p = 0,249	H_0 is not rejected
SO_Max	F = 1,63, p = 0,224	H_0 is not rejected
Max_FC	F = 1,23, p = 0,317	H_0 is not rejected
FC_PS	F = 0,63, p = 0,545	H_0 is not rejected

Transport_1	**one-way analysis of variance (one-way ANOVA)**	**post hoc analysis (Bonferroni)**
Baseline_SO	F = 3,54, p = 0,049	subadults > females *
SO_Max	F = 0,7, p = 0,509	H_0 is not rejected
Max_FC	F = 2,27, p = 0,13	H_0 is not rejected
FC_PS	F = 5,87, p = 0,01	subadults > males * subadults > females *

Transport_2	one-way analysis of variance (one-way ANOVA)	post hoc analysis (Bonferroni)
Baseline_SO	F = 0,2, p = 0,818	H_0 is not rejected
SO_Max	F = 6,04, p = 0,01	subadults > males * subadutls > females **
Max_FC	F = 7, p = 0,006	subadults > males * subadutls > females **
FC_PS	F = 5,26, p = 0,016	subadults > males * subadutls > females **

*Angle measurements – statistical analysis comparing the two different feeds (*Acheta domesticus *&.* Galleriinae)

The following description sums up the significant, and therefore important angle-change measurements of the three individual groups (males, females and subadults) while comparing them between the two different prey items (*Acheta domesticus* and *Galleriinae*).

Comparing the two different feeds in males:

In all phases of the capture and manipulation_1 cycle the Levene test of equality of variance yields a p-value above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. A two-tailed t-test for independent samples (equal variances assumed) showed that the difference between the two prey items was not statistically significant with respect to the dependent variable (each phase). The h_0 is thus retained in all phases.

In the manipulation_2 cycle the phase “SO_Max” showed in the Levene test a p-value of <0.001, which is below the 5% significance level. The Levene test is therefore significant and the h_0 that all variances of the groups are equal is rejected. The two-tailed t-test for independent samples (equal variances not assumed) showed that the difference between two prey items with respect to the dependent variable SO_Max was statistically significant, t(8,08) = -2.34, p = 0.047, 95% confidence interval [-8.74, -0.06]. The h_0 is thus rejected. (*Galleriinae* > *Acheta domesticus*)

In the manipulation_2 cycle the phase “Max_FC” showed in the Levene test a p-value of 0.939, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. A two-tailed t-test for independent samples (equal variances assumed) showed that the difference between the two prey items with respect to the dependent variable Max_FC was statistically significant, t(26) = -2.36, p = 0.026, 95% confidence interval [-5.64, -0.39]. The h_0 is thus rejected. (*Galleriinae* > *Acheta domesticus*)

In the manipulation_2 cycle the phase “FC_PS” showed in the Levene test a p-value of 0.015, which is below the significance level of 5%. The Levene test is therefore significant and the h_0 that all variances of the groups are equal is rejected. The two-tailed t-test for independent samples (equal variances not

assumed) showed that the difference between the two prey items with respect to the dependent variable FC_PS was statistically significant, t(7.92) = -2.95, p = 0.019, 95% confidence interval [-7.84, -0.95]. The h_0 is thus rejected. (*Galleriinae* > *Acheta domesticus*)

In the transport_1 cycle the phase "Max_FC" showed in the Levene test a p-value of 0.73, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. The two-tailed t-test for independent samples (equal variances assumed) showed that the difference between two prey items with respect to the dependent variable Max_FC was statistically significant, t(26) = -2.15, p = 0.041, 95% confidence interval [-5.82, -0.13]. The h_0 is thus rejected. (*Galleriinae* > *Acheta domesticus*)

In the transport_1 cycle the phase "FC_PS" showed in the Levene test a p-value of 0.941, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. A two-tailed t-test for independent samples (equal variances assumed) showed that the difference between the two pray items with respect to the dependent variable FC_PS was statistically significant, t(25) = -2.53, p = 0.018, 95% confidence interval [-5.72, -0.58]. The h_0 is thus rejected. (*Galleriinae* > *Acheta domesticus*)

In the transport_c cycle the phase "FC_PS" showed in the Levene test a p-value of 0.187, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. The two-tailed t-test for independent samples (equal variances assumed) showed that the difference between cricket and maggot with respect to the dependent variable PS was statistically significant, t(26) = -2.84, p = 0.009, 95% confidence interval [-4.48, -0.72]. The h_0 is thus rejected. (*Galleriinae* > *Acheta domesticus*)

Comparing the two different feeds in females:

In the capture cycle the phase "FC_PS" showed in the Levene test a p-value of 0.943, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. The two-tailed t-test for independent samples (equal variances assumed) showed that the difference between the two prey items with respect to the dependent variable FC_PS was statistically significant, t(26) = -2.34, p = 0.027, 95% confidence interval [-8.41, -0.54]. The h_0 is thus rejected. (*Acheta domesticus* > *Galleriinae*)

In all phases of the manipulation_1 cycle the Levene test of equality of variance yields a p- above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained.

In the manipulation_2 cycle the phase “FC_PS” the Levene test showed a p-value of 0.118, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. A two-tailed t-test for independent samples (equal variances assumed) showed that the difference between the two prey items with respect to the dependent variable FC_PS was statistically significant, t(24) = -2.39, p = 0.025, 95% confidence interval [-6.11, -0.45]. The h_0 is thus rejected. (*Acheta domesticus* > *Galleriinae*)

In the transport_1 cycle the phase “baseline_SO” the Levene test yields a p-value of 0.106, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. The two-tailed t-test for independent samples (equal variances assumed) showed that the difference between the two prey items with respect to the dependent variable baseline_SO was statistically significant, t(26) = 2.48, p = 0.02, 95% confidence interval [0.5, 5.34]. The h_0 is thus rejected. (*Acheta domesticus* > *Galleriinae*)

In all phases of the transport_2 cycle the Levene test of equality of variance yields a p- above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. (*Galleriinae* > *Acheta domesticus*)

Comparing the two different feeds in subadults:

In the capture cycle the “FC_PS” phase showed in the Levene test a p-value of 0.241, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. The two-tailed t-test for independent samples (equal variances assumed) showed that the difference between the two prey items with respect to the dependent variable FC_PS was statistically significant, t(22) = -3.69, p = 0.001, 95% confidence interval [-12.67, -3.55]. The h_0 is thus rejected. (*Galleriinae* > *Acheta domesticus*)

In the manipulation_1 cycle the phase “Max_FC” showed in the Levene test a p-value of 0.478, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. The two-tailed t-test for independent samples (equal variances assumed) showed that the difference between the two prey items with respect to the dependent variable Max_FC was statistically significant, t(24) = -2.33, p = 0.028, 95% confidence interval [-9.92, -0.61]. The h_0 is thus rejected. (*Galleriinae* > *Acheta domesticus*)

The F”C_PS” phase in the Levene test yields a p-value of 0.899, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. The two-tailed t-test for independent samples (equal variances assumed) showed that the difference between the two prey items with respect to the dependent variable FC_PS was statistically

significant, t(24) = -3.05, p = 0.005, 95% confidence interval [-11.16, -2.16]. The h_0 is thus rejected. (*Galleriinae* > *Acheta domesticus*)

In the manipulation_2 cycle the phase "baseline_SO" showed the Levene test showes a p-value of 0.248, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. The two-tailed t-test for independent samples (equal variances assumed) showed that the difference between the two prey items with respect to the dependent variable baseline_SO was statistically significant, t(21) = -3.72, p = 0.001, 95% confidence interval [-6.16, -1.74]. The h_0 is thus rejected. (*Galleriinae* > *Acheta domesticus*)

In the transport_1 cycle the "baseline_SO" phase shows in the Levene test a p-value of 0.206, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. The two-tailed t-test for independent samples (equal variances assumed) showed that the difference between the two prey items with respect to the dependent variable baseline_SO was statistically significant, t(23) = -2.53, p = 0.019, 95% confidence interval [-4.12, -0.41]. The h_0 is thus rejected. (*Galleriinae* > *Acheta domesticus*)

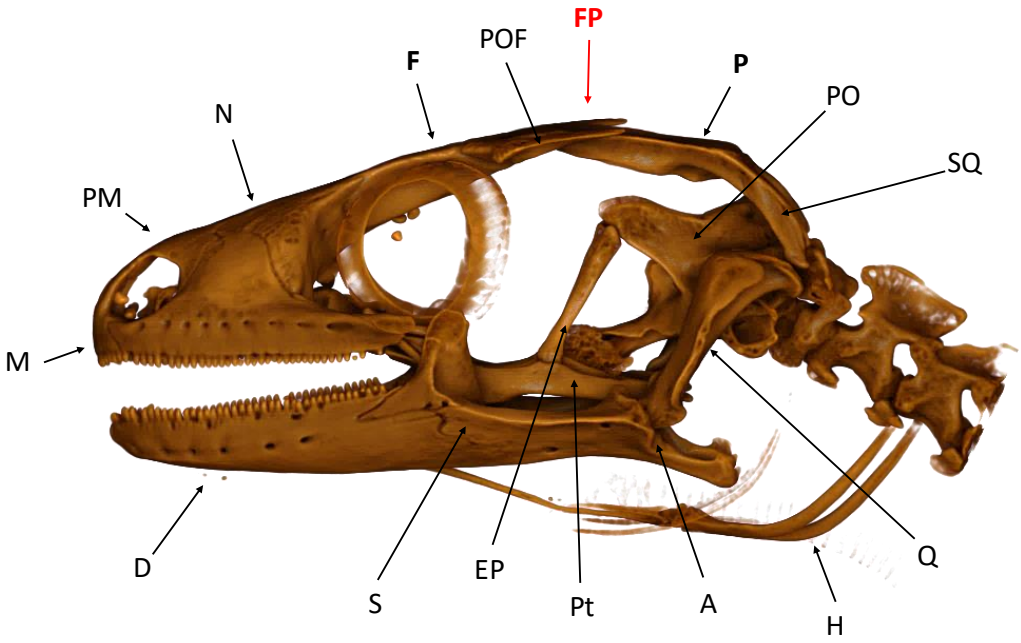
The "FC_PS" phase in the Levene test yields a p-value of 0.949, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. The two-tailed t-test for independent samples (equal variances assumed) showed that the difference between the two prey items with respect to the dependent variable FC_PS was statistically significant, t(23) = -2.44, p = 0.023, 95% confidence interval [-10.47, -0.85]. The h_0 is thus rejected. (*Galleriinae* > *Acheta domesticus*)

In the transport_2 cycle the "FC_PS" phase shows in the Levene test a p-value of 0.916, which is above the significance level of 5%. The Levene test is therefore not significant and the h_0 that all variances of the groups are equal is retained. The two-tailed t-test for independent samples (equal variances assumed) showed that the difference between the two prey items with respect to the dependent variable FC_PS was statistically significant, t(22) = -4.91, p = <0.001, 95% confidence interval [-9.11, -3.7]. The h_0 is thus rejected. (*Galleriinae* > *Acheta domesticus*)

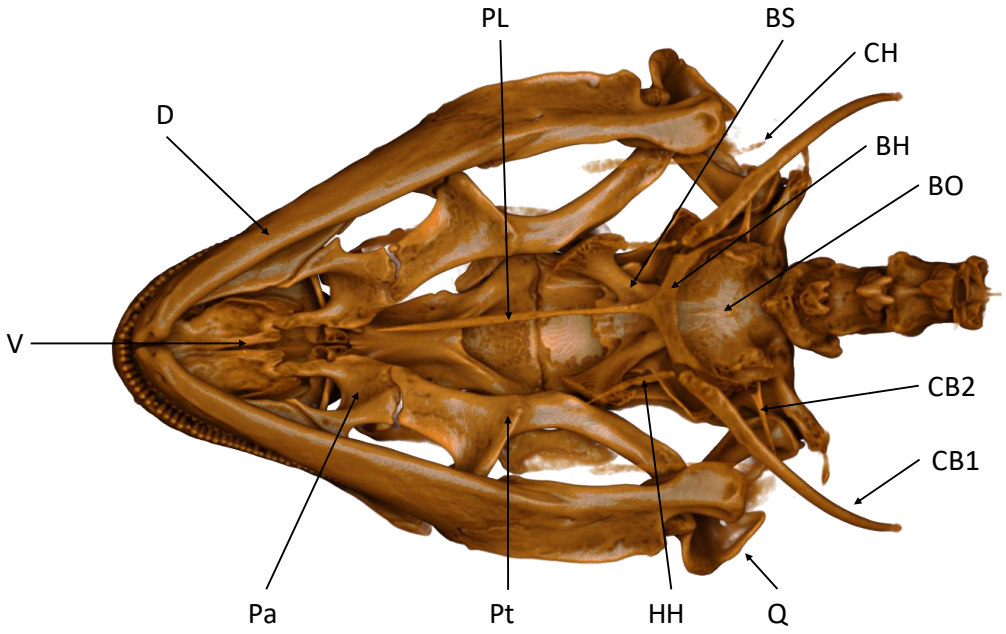
Skull morphology: description of the skull based on the microCT scans

The 3D visualization (Fig. 6) shows the delicate cranial osteology of *Eublepharis macularius*. A large quadrate, which appears to be clearly mobile, offers a large attachment surface for musculature. The jugal is absent and the postorbital and the squamosal is strongly reduced, so the superior temporal arch is reduced. Thus, the superior temporal fenestration is also missing. The fronto-parietal suture is located slightly behind the orbit and is well visible and smooth. The animals have a very large orbit.

A



B



C

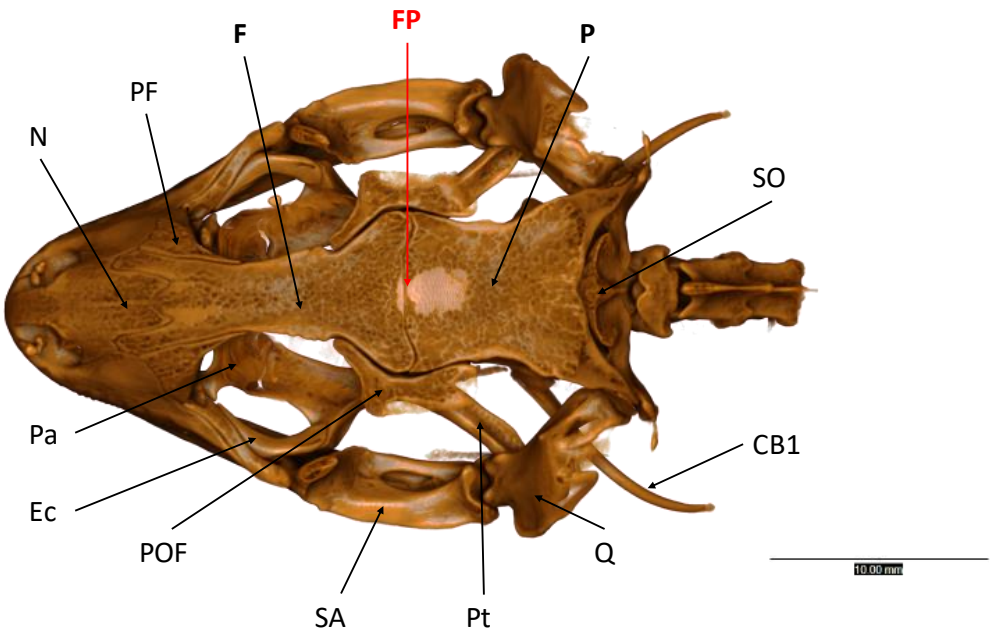


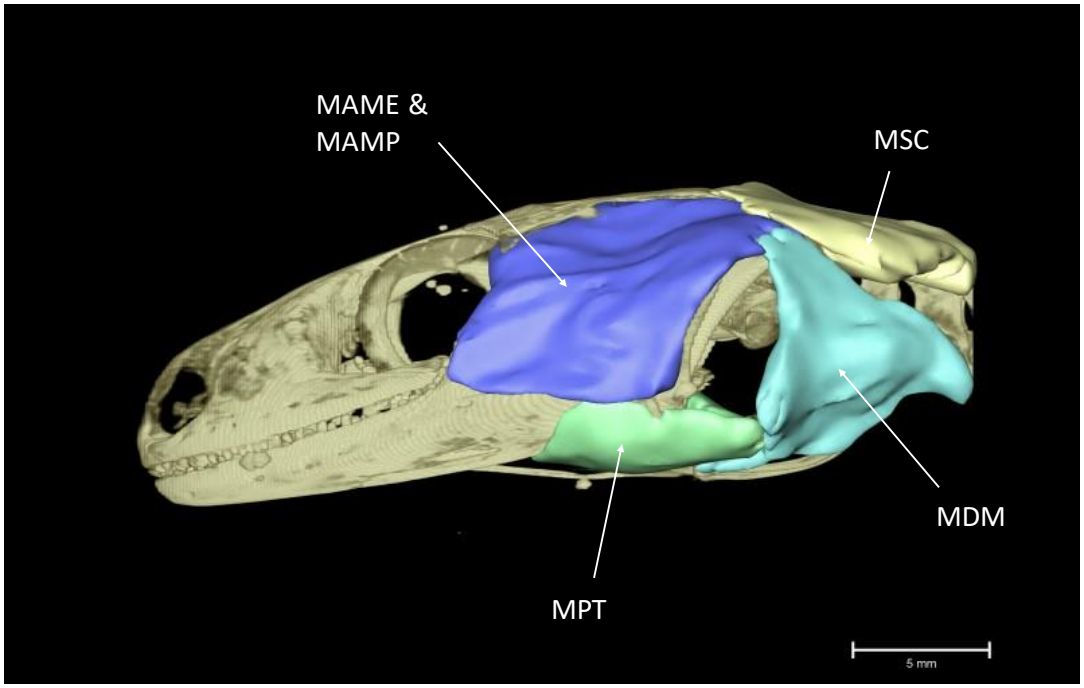
Figure 6 Cranial osteology of Eublepharis macularius *based on volume rendering of microCT. (A) Lateral View. (B) Ventral view. (C) Dorsal view. (A) Articular, (BH) Basihyale (BO) Basioccipital, (BS) Basisphenoid, (CB 1&2) Ceratobranchiale 1&2, (CH) Certohyale, (D) Dentary, (EP) Epipyterygoid, **(F) Frontal, (FP) Fronto-parietal suture,** (H) Hyoid, (HH) Hypohyale, (M) Maxilla, (N) Nasal,, **(P) Parietal**, (PF) Prefrontal, (POF) Postorbitofrontal, (PL) Processus lingualis (PM) premaxilla, (PO) prooticum, (Pt) Pterygoid, (Q) Quadrate, (SO) Supraoccipital, (SQ) Squamosal, (V) Vomer. Scale bar is 10mm.*

Image segmentation

The description of the image segmentation of the skull musculature only includes the muscle groups that are important for the feeding process.

Posterior to the musculus adductor mandibulae externus (MAME) lies the m. adductor mandibulae posterior (MAMP). The MAME originates at the ventral surface of the postorbitofrontal and supratemporal and the lateral part of the parietal; and the MAMP originate at the quadratum. Both insert at the mandible. In this specific dual-scan they can‘t be distinguished, therefore they were illustrated together. The image segmentation shows that the MAME together with the MAMP are by far the most voluminous muscles in the skull. They connect the mandible to the ventral surface of the parietal and postorbitofrontal. The m. depressor mandibulae (MDM) runs from the lateral part of the parietal into the retroarticular process of the mandible. The m. pterygoideus (MPT) lies deep to the MAME. It begins at the pterygoid and ends to the angular, surangular, articular and retroarticular process. The m. spinalis capitis (MSC) originates along the vertebrae and inserts along the posterior part of the parietal. The m. levator pterygoideus (MLPT) originates from the ventral surface of the parietal and inserts at the pterygoid. The m. protractor pterygoideus (MPPT) runs from the occipital region and the m. pseudotemporalis (MPST) starts at the ventral part of the parietal. Both insert to the pterygoid. (see figure 7)

A



B

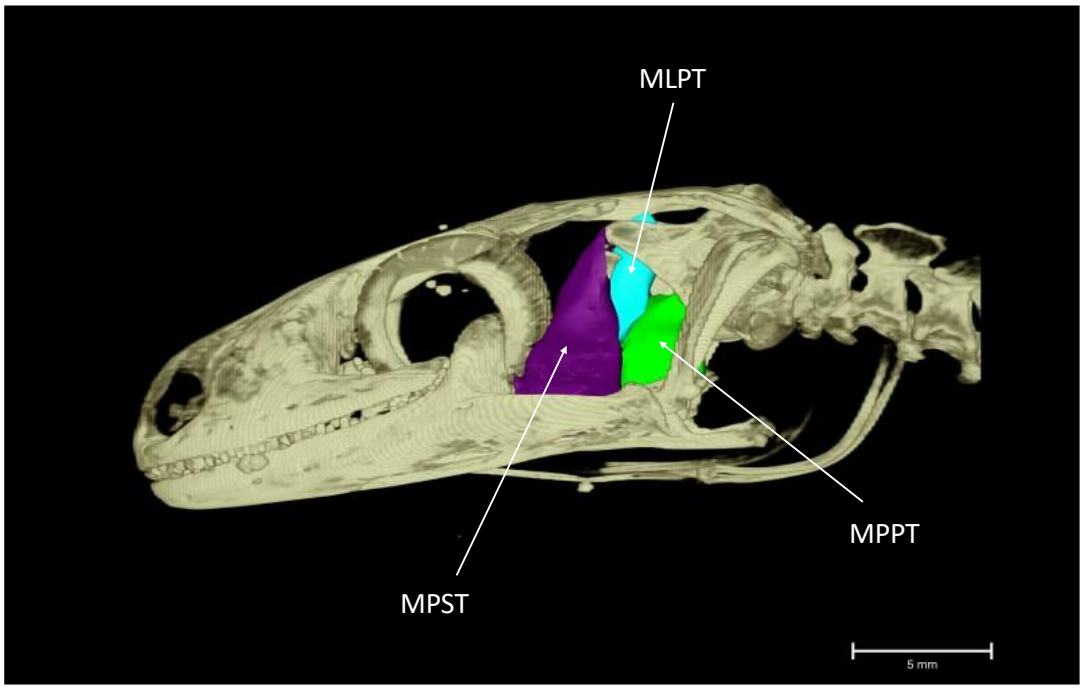


Figure 7 Cranial musculature imaging of Eublepharis macularius. (A) Lateral view. (B) Lateral view with external musculature removed. *(MPPT) m. protractor pterygoideus, (MLPT) m. levator pterygoideus, (MAME) m. adductor mandibulae externus, (MAMP) m. adductor mandibulae posterior, (MPST) m. pseudotemporalis, (MPT) m. pterygoideus, (MSC) m. spinalis capitis, (MDM) m. depressor mandibulae. Scale bar is 5mm.*

Muscle volumes

The volume analysis of the reconstructed cranial musculature confirms the visualization; MAME and MAMP together represent the most voluminous muscles in the skull. MSC as second and MPT as third voluminous muscles represent to more or less identical strong muscles. The final 20 % of the muscles are subdivided into four smaller muscles (MPPT, MLPT, MPST and MDM) (see table 15).

Table 15 Absolute mean volumes and percentage (relative volumes) of the reconstructed musculature in the skull of Eublepharis macularius.

Material	mean Volume (mm^3)	%
MAME & MAMP	175,095	51%
MSC	59,394	17%
MPT	43,279	13%
MDM	23,921	7%
MPPT	20,383	6%
MPST	9,464	5%
MLPT	6,207	2%

Discussion

This study provides an anatomical, morphological and experimental analysis of the intracranial movements of the gecko *Eublepharis macularius*. In detail, high speed cinematography, 3D visualization of microCT scans, image segmentation and muscle reconstruction were provided and analyzed. The three groups (males, females and subadults) were fed with two different prey items (*Acheta domesticus* and the wax moth larvae of *Galleriinae*) to compare not only the sexual dimorphism and the age differences, but also the behavior towards different preys.

Animals: For a successful comparison of the three groups (males, females and subadults), it was important to distinguish between adult and subadult properties. Analyzing the size, general behaviour and especially the dataset of the two subadult individuals, it seems that there is enough evidence that both are still in their growth phase. They didn't reached their final size yet, so they shouldn't have already ossified completely. Therefore the comparison between adult and subadult can be done.

Video Analysis: The intention of the two different prey items was to detect, if the leopard geckos differentiate between two preys of different texture, mobility and consistency. On the one hand, *Acheta domesticus* is a fast and mobile animal (fast movements and reflections) and has a more or less hard body with "bulky" legs and wings. On the other hand, the larvae of *Gallerinae* is in a slow moving life stage, with a smooth and soft body. By choosing these two prey items, some differences in the feeding behaviour were expected.

The capture cycle during the food consumption of both preys, requests the greatest distance between the upper and lower jaw (see figure 4). This can be explained by the fact, that the capture of a prey has to be "overcalculated" to not lose the potentially prey. In this cycle the individual has to coordinate the own cranial movement and the possible flight attempt of the prey. This leads to the assumption that a higher mouth opening is necessary during the prey cycle. The adult males showed in the capture cycle the highest peak (the greatest distance between upper and lower jaw) of all three groups. This can be explained by the absolute body size of the male individuals in relation to the others (see table 2). Interestingly, the capture cycle is the only cycle without a slow opening phase. This can be possibly explained by the approach phase and the time constraints. During the capture cycle the predator should not lose time and thus possibly lose his prey. The same observation was done in a similar study with the day gecko *Phelsuma madagascariensis*, where again no SO phase was detected during the capture phase (Delheusy & Bels, 1999). In the mesokinetic scincid species *Ablepharus kitaibelii* only 50% of similar analyzed videos, a SO phase during the capture cycle was detected (Handschuh et al., 2019). This is in big contrast to lizards using tongue-based prehension, that show clearly the SO phase in the capture cycle, as a preparation before they eject their tongue (Herrel et al., 1996; Meyers & Herrel, 2005)

The phases of manipulation and transport, on the other hand, show smaller gapes but on the other hand the angel change in the fronto-parietal-suture is higher in these cycles. This indicates that the lower jaw is not lowered as much after the capture cycle, but the kinetic deflection is increased. This indicates, that the mouth-opening is more effected by the cranial elements, than by the depression of the lower jaw. It is necessary for the individual not to open the mouth completely as it may could happen, that the captured prey is flexible and still alive enough to escape from the open mouth. In addition, not opening the mouth at its maximum, saves energy. A slow opening phase is detectable in the manipulation and transport cycles. Important to say here is, that even with a well-defined definition of the SO phase, the detection is quite difficult and depends a lot of the individual preference of the analyzer. This makes a comparison between different studies harder and unreliable. However, it is in general debatable if the SO phase should be considered and analyzed in such studies. In the present study the SO phase was always detected but the standard deviation of the duration of the SO phase in each cycle is high and varies a lot.

The same results can be observed for the food intake of *Galleriinae* (figure 5). The only difference to mention is the total and the specific duration of each cycle and phase, which will be discussed in more detail below. The peaks and the structure of each cycle were similarly patterned as the ones during feeding on *A. domesticus*.

Approach to the prey: The adult male and female show a higher maximal velocity in the *A. domesticus* prey approach, than in the *Galleriinae* (see table 3 and 4). This is in alignment with studies on varanids, where differences between elusive and immobile prey were detected (Montuelle et al., 2012a, 2012b). This could be an indicator that the animals distinguish between a fast and unpredictable mobile prey (*A. domesticus*) and a slow and more or less motionless prey like the *Galleriinae*. A quick approach to the prey guarantees the best chance to chase the fast prey. Whereas the motionless wax moth larvae can't escape from the predator. With respect to the approach, the subadults don't show any significant differences between the two prey items, even though the absolute measured mean values show a higher max. vel. (5) during the food consumption of *Acheta domesticus*. That could be explained by the missing experience of the younger individuals with different prey items.

Duration and Velocity: Comparing the three groups consuming *A. domesticus,* one can see that the adult males have the highest duration of each phase in the transport_1 cycle and the subadults the lowest. Also in other cycles (except the capture cycle) the adult male has the highest duration. This could possibly be explained by the difference in the skull size. The males have, due to their general larger body size, a longer distance from the total mouth closing to the total mouth opening or vice versa. Recovering this distance costs time, represented by the duration. Nevertheless, there is no clear analytical pattern between the three groups. Regarding the first explanation, the adult females should

then always have the second longest duration time, as they are only a little bit smaller than the adult males and bigger than the subadults, but that is not given. Here an extended explanation could be introduced. Sexual dimorphism is slightly given in this species. The females of lizards in general are not only a bit smaller in size than the males, but also the muscle proportions are different, especially the muscles involved in jaw movement and biting. The data analysis of wall lizards confirmed that those muscles can be an important element of sexual dimorphism in lizards (Urošević et al., 2012). These larger muscles play an important role in territoriality, female choice and mating (Herrel et al., 1999, 2007; Ljubisavljević et al., 2010, 2011). Therefore, the male leopard geckos could be faster in there jaw movement than the one of females, caused by their natural difference in muscle size and structure. Hence the females show similar duration and velocity patterns as the subadults.

Comparing the three groups during the consumption of *Galleriinae* there is no clear structure at all. But again the males reach in all cycles the highest duration time and also the fastest mean velocity, except in the fast closing phase of the capture where the subadults are significantly faster than the adult females and males. The missing differences in this statistical analysis could be an indicator that the more or less motionless prey is for none of the individuals a challenge and they don't have to be consistent and firm during the feeding cycle.

Comparing the two prey items the adult males have no recognizable pattern in their dataset. This is probably caused by the high SD in both situations. However the females and juveniles showed some clear structure in all cycles. In most of the phases the duration when feeding on *Galleriinae* was lasting significantly longer than with *A. domesticus*. Whereas the Individuals showed higher mean velocities and maximal velocities when consuming *A. domesticus* comparing to the *Galleriinae*. This would fit perfectly with the assumption that the wax moth larvae as soft and more or less motionless prey needs less speed during the phases. On the other hand the *A. domesticus* has a hard sclerotized structure and is fast in his movement. Therefore the predator has to be quicker and faster during the phases and needs also less time (duration) in each phase. If one looks closely at the data, one can see that adult males also follow this hypothesis and consume *Acheta domesticus* faster than the larvae of *Galleriinae*. However, the unusually long SO phases distort the results and thus influence the statistics. This could be another indication that the SO phases bias the analysis of such studies.

Comparing the transport cycle dataset (food intake of *A domesticus*) with the presented data of *Phelsuma madagascariensis* and *Gekko gecko* by Herrel and colleagues (1999), it is notable that the duration of all transport phases measured in the present study with *Eublepharis macularius* are similar to the one of *Phelsuma madagascariensis.* The only exception is the SO-phase. Herrel and colleagues divided in their study the slow opening phase into SOI and SOII. This subdivision is based on the jaw and tounge movements, therefore it can't be compared. As these two species don't share the same

habitat and distribution or the same behaviour and ecology, this similarity has to arise from a phylogenetic relationship.

Angle measurements: All three groups showed in all phases of all cycles a measurable angle change. The presence of mesokinesis could thus be proven for all six individuals. Especially the angle changes in the prey-catching phase show strong differences in all individuals. The standard deviations are in some cases relatively high; above all in the whole capture cycle. The high SD in the capture cycle can be attributed to the fact that the animals frequently changed their movement patterns and alternated the distance from upper to lower jaw depending on the situation (size and position of the prey) and did not show any regularity, resulting in extreme values that influenced the statistical analysis.

Comparing the three groups during the food consumption of *A. domesticus,* one can see that there are no significant differences between the groups in the manipulation_1 cycle as well as in the transport_2 cycle. Transport_2 could be explained by the fact that it happens most of the time at the end of a feeding cycle (before the swallowing starts) where the prey has already changed its shape (through the manipulation processes before) and probably is already dead. In this cycle, the power of each phase has no longer to be so strong, for example the PS was actually not detected and therefore seems to not be needed. The explanation for manipulation_1 is more uncertain. The manipulation_1 is mostly right after the capture cycle. Here, the prey could be still alive and escape out of the mouth of the individual. To avoid this, all three groups handled the situation the same way. The only really high significant difference between the three groups where the angle change between the FC- and the PS-phase. The subadults show here a higher angle change than the adult males and females. The power stroke at the end of each cycle is a powerful squeezing of the upper and lower jaws, which is accompanied by extreme muscle tension by the adductor muscles (MAME, MPST and MPT) and this power causes an extreme angle change (Herrel et al., 1999). The subadults are not fully grown yet, so their ossification is ongoing and this enables them to show higher mesokinetic angle change than the adults.

During the food intake of *Galleriinae,* the subadults showed again the highest angle change in the fronto-parietal suture between the FC- and the PS-phase. Especially the transport_2 phase is here of bigger interest. In contrast to the food consumption of *A. domesticus,* the data showed here high significances between the three groups. The subadults showed in all phases of the transport_2 cycle a significant higher angle change than the adult males and females. As this is in contrast to the previous explanation of this cycle, it's important to add that feeding on *Galleriinae* required in nearly all cases a higher angle change than *Acheta domesticus*. This is sustained by the analysis of the prey differences. All three groups, especially the subadults, showed in almost all phases of all cycles a significant higher angle change in the fronto-parietal suture with the *Galleriinae*, than with the *A. domesticus.* Here again

is to mention that the females provide one exception in the transport_1 cycle. The angle change between the baseline and the slow opening phase is significantly higher when feeding on *A. domesticus*. Whereas the fast closing phase of all cycles showed always high angle changes in all individuals. The reason for this is probably the fact that in this phase they really use their cranial muscle power to bite and therefore the change in the fronto-parietal suture is higher. The soft texture of the wax moth larvae allows more "chewing" and it needs also more stabilization because of the smooth surface. This could be a possible explanation why the *Gallerinae* request, not only in the FC-PS-phase, but also in all other phases a significant higher angle change. Montuelle and Williams showed in 2015 in their in vivo study of *Gekko gecko* not only mesokinetic movement patterns, similar to those detected in this study, but were also able to identify other movements in the cranial region. In their study, they investigated the cranial elements not only during feeding, but also during defense against a predator. They figured out that the defensive bite forces in *Gekko gecko* are significantly lower, in comparison to other lizards, and it has been suggested to be related to the presence of cranial kinesis. They found a positive correlation between the ventral flexion of the snout and bite force indicating that the harder the individual bites, the more ventral flexion is given. Similar to their study, the associated mesokinetic displacement during a feeding cycle over time shows his maximum change at the FC-PS-Phase in our recordings. Hence, the highest angle change in the fronto parietal suture is shown when the maximum ventral flexion of the snout relative to the braincase is given. Comparing the skull structure and the data of *Eublepharis macularius* with the published data of the sister group *Gekko gecko*, it is reasonable to assume that *E. macularius* shows similar movement patterns in vivo. The data of Herrel and colleagues (1999) also showed some similarities of the two species *Phelsuma madagascariensis* and *Gekko gecko*. Here, the data of *Eublepharis macularius* would perfectly fit within the concept of these two species.

Reports of previous studies indicate that juvenile stages have higher kinetics than adult stages (Barahona & Barbadillo, 1998; Starck, 1979). This can be explained by the fact that during ontogenesis the vertebrate bones harden and fuse only in a second moment and thus the skeleton loses flexibility. The studies by Anderson Maisano (2002) on *Lepidophyma gaigeae* and four *Xantusia* taxa (Scincoidea, Squamata) would suggest such an assumption. The recent study seems to extensively support this hypothesis. The subadults showed in most of the cases higher angle changes than the adult males and females.

The data of the three groups of *Eublepharis macularius* do not show the maximum possible deflection of the fronto-parietal suture of these highly kinetic animals, but only the cranial movements appropriate for the prey. These deflection minima are, from an evolutionary point of view, energetically appropriate. The recorded extreme values from the video material (e.g. maximum

measured extreme value of +18° (dorsal flexion) and -37° (ventral flexion) in the subadults capture cycle of *Galleriinae*) show, that a higher deflection at the fronto-parietal suture is however possible. In order to be able to describe the actual maximum deflection, the animal would have to be provided with a prey large enough to trigger the maximum value.

Skull morphology: *Bellairsia gracilis*, the oldest known squamate, had a large robust jugal (Tałanda et al., 2022). Compared to the ancestor, the jugal of *Eublepharis macularius* is completely reduced, as in all *Gekkota* (Herrel et al., 2007). The cranial morphology of *Eublepharis macularius* shows a lightweight construction for increased flexibility (Hernández Morales et al., 2019). This allows greater freedom of movement of the entire anterior cranial region (Herrel et al., 2007). The jugal is absent, the squamosal is strongly reduced, thus the superior temporal arch and the superior temporal fenestration is missing. This enormous reduction leads to this already mentioned lightweight construction and a relative open skull structure. Among modern Squamata the reduction in size of specific cranial elements and at the same time including moving joints is typically associated with cranial kinesis (Herrel et al., 2007; Metzger, 2002; Schwenk, 2000). The quadratum is long and also relatively broad and provides a large attachment surface for strong and distinct muscles for feeding (M. Adductor mandibulae posterior), similar to the quadratum of *Ablepharus kitaibelii* (Handschuh et al., 2019), *Oedura lesueurii*, *Hemitheconyx caudicinctus*, *Tarentola annularis* and *Chondrodactylous bibronii* (Payne et al., 2011), as well as *Sphaerodactylus roosevelti* (Daza et al., 2008), *Gekko gecko* and *Phelsuma madagascariensis* (Herrel et al., 2000). Due to the morphology of the quadratum and its articulation to the exoccipital (dorsal) and articular (ventral), it appears to be very mobile, so streptostyly occurs to a considerable extent. The enlarged quadrate shell evolved early (for example in *Paliguana*) simultaneously with the reduction of the quadratojugal and the loss of the lower temporal bar (Evans, 2003). Already in *Bellairsia*, a stem lizard, streptostyly could be detected and therefore it seems to be a plesiomorphic characteristic (Tałanda et al., 2022). However, without data from the Triassic phylum of Squamata, the stages of evolution of streptostyly cannot be outlined. The group Gekkota became nocturnal early in evolution and thus developed a larger orbit for better vision, and so did also *Eublepharis macularius* (Franz-Odendaal, 2020; Schmitz & Motani, 2010). This large orbit needs space in the skull, which is given by the reduction of the jugals and postorbitals. Other nocturnal Gekkota like *Sphaerodactylus roosevelti* did not completely reduce the jugal and postorbital, even though the orbit makes 30% of the skull, but did not entirely surround it by bones (Daza et al., 2008). The fronto-parietal suture of the leopard gecko lies caudal to the orbit and is well defined. This fronto-parietal suture is smooth and allows elevation of the snout (frontals, nasals, maxillaries, premaxillaries, and some others) relative to the posterior region of the skull roof (parietals). In mesokinetic species like *Eublepharis macularius* the dermatocranium is slightly lowered (and thus the skull is flattened) when the mouth is opened (see figure 6) .Bellairsia doesn't show this features and it was suggested, that mesokinesis was not yet

developed (Tałanda et al., 2022). So, streptostyly was already present at the beginning. When the geckos separated they adapted to nocturnal activities and other specializations by reduction in several cranial bones which in the end led to mesokinesis (For review see: Metzger, 2002). The mesokinetic cranial structure of *Eublepharis macularius* is consistent with the conclusion of Herrel et al.´s study on geckos (2000), that cranial kinetics in geckos is not an adaptive trait but a consequence of cranial structure. The high flexibility, which is due to the loss of the jugal bar and the reduction of the postorbital compensates for the negative consequences; these would be the reduced biting force and the fragility.

Image segmentation: The functional roles of the cranial musculature packages during a feeding cycle in gekkonid lizards had already been described by Herrel and colleagues in 1999. Following their electromyographic description of the species *Gekko gecko* and *Phelsuma madagascariensis* many similarities can be observed. Like in other squamates, *Eublepharis macularius'* depression (mouth opening) is carried out by the action of the MDM. MDM contracts and this opens the mouth by pulling down the lower jaw. Simultaneously, the protraction of the pterygoid may be actively reinforced by action of the MPPT. This protraction of the basal cranial elements leads to an extension of the frontal (+ nasal, premaxillae, maxillae, septomaxillae, vomers, prefrontal and lacrimal). The quadrate rotation occurs as a direct consequence of depression of the mandible and this rotation drives the protraction of the pterygoid as well. This quadrate movement forwards can be noted as streptostyly. According to Herrel's investigations, the inactivity (release of tension) of the MPPT alone would be enough to return the cranial system to its neutral position (Herrel et al., 1999). During the active phase of these two muscles the MSC elevates, by contraction, the parietal bone. This contraction seems to be necessary for the protraction of the pterygoid (Smith & Hylander, 1985).

Mouth closing involves the action of several muscles. However, with advancing mandible elevation and reduced distance between the upper and the lower jaw, MAME together with MAMP seem to be the most important muscles. They close the mandible while the MPT and the MPST retract the pterygoid. Following Herrel's study (1999), they should show their highest activity during the PS phase. During mouth closure these muscles together elevate the mandible and cause a ventral flexion in the fronto-pariental suture (mesokinetic movement) by retraction of the pterygoid (Frazzetta, 1962; Iordansky, 2011).

So, the extension of the frontal bone by MDM and MPPT (forward movement of the pterygoid by quadrate rotation or muscle contraction) and the elevation of the parietal bone by the MSC cause together the angle change in the fronto-parietal suture (the mesokinetic movement), during mouth opening.

Muscle volumes: Sustaining the image segmentation, the muscle volume analysis shows that the MAME and MAMP form the biggest muscle in the cranial part of the *Eublepharis macularius*. Followed by MSC and MPT. In the study by Handschuh and colleagues in 2019 of the miniaturized skink *Ablepharus kitaibelii,* the measurements of the muscle volumes show slightly different percentages. Even though, the MAME and MAMP are in both studies the most voluminous ones and represent more or less 50% of all analysed muscles, the MSC was not analysed by Handschuh et al. (2019). MLPT was the smallest muscles in both studies, but in *A. kitaibelii,* MPST is larger than in *E. macularius* (Handschuh et al., 2019). Differences in the muscle volumes could derive from individual muscle development of the analyzed animals during their life span (growth speed, nutrition, light exposure, inter- and intraspecific competition ect.) but also from differences in conservation time, dehydration or scan-quality (Buytaert et al., 2014).

Conclusion: The evaluation of the movement patterns, the 3D visualizations and the image segmentation lead to the assumption that *Eublepharis macularius* is a highly kinetic *Gekkota* species. It can be confirmed with certainty that *Eublepharis macularius* shows streptostyly and mesokinesis. The morphological structure of the skull could possibly also be suitable for metakinetic movements. This would mean that *Eublepharis macularius* has an amphikinetic skull. In further studies, this could be confirmed with the help of XROMM analyses, in vivo X-ray films and computer simulations.

Zusammenfassung

Betrachtet man die intrakraniellen Bewegungen während der Nahrungsaufnahme, so spricht man von der sogenannten Schädelkinetik. Diese Bewegungen innerhalb des Schädels von Wirbeltieren erfolgen unabhängig vom Unterkiefer, dem Mittelohr und dem Hypobranchialskelett. In Bezug auf diese Bewegungen gibt es einige wichtige Begriffe, darunter Mesokinese, Metakinese, Amphikinese und Streptostylie. In der vorliegenden Studie wurden die intrakraniellen Bewegungen des Geckos *Eublepharis macularius* untersucht. Anhand anatomischer, morphologischer und experimenteller Daten, die auf Hochgeschwindigkeitskinematographie und 3D-Visualisierung von Mikro-CT-Scans, Bildsegmentierung und Muskelrekonstruktion beruhen, haben wir zwei adulte Männchen, zwei adulte Weibchen und zwei subadulte Tiere (ein Männchen und ein Weibchen) bei der Fütterung mit zwei verschiedenen Beutetieren (*Acheta domesticus* und Wachsmottenlarven der *Galleriinae*) verglichen. Mesokinese wurde mittels Hochgeschwindigkeitskinematographie in allen drei Gruppen mit beiden Beutetieren während des Beutefangs, der oralen Manipulation und des oralen Transports nachgewiesen. Die Daten deuten außerdem auf ein hohes Potenzial für Amphikinese und Streptostylie hin. Der Vergleich zwischen den beiden Beutetieren ergab Unterschiede in der Dauer und Geschwindigkeit des Fresszyklus. Darüber hinaus wirken sich die beiden Beutetiere unterschiedlich auf die intrakraniellen Bewegungsmuster aus. Im Vergleich der drei Gruppen zeigten die subadulten Tiere die höchste Flexibilität an der Fronto-Parietal-Naht (mesokinetischer Winkel). Auch hinsichtlich der Geschwindigkeit und Dauer der einzelnen Zyklen konnten Unterschiede zwischen den drei Gruppen festgestellt werden. Die Analyse der Muskelvolumina zeigte, dass die anterioren und posterioren Adduktoren zusammen den größten Muskelanteil im Schädel bilden. Insgesamt zeigen die vorgelegten Daten, dass *E. macularius* eine hoch kinetische Art innerhalb der basalen Gruppe der Gekkota ist.

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