

# Feeding Behaviour and Feeding Motorics in Subadult European Pond Turtles, *Emys orbicularis* (Linnaeus, 1758)

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**Abstract:** The European Pond Turtle is a predominantly aquatic species, generally assumed to feed exclusively under water by using hydrodynamic mechanisms. We analysed the kinematics of the aquatic food uptake and food transport by using high-speed videos with 500 fps. The analyses revealed that subadult *E. orbicularis* use compensatory suction for food uptake, but the food transport is performed by a combination of compensatory and inertial suction mechanisms. In contrast to other aquatic and semi-aquatic testudinoids studied to date, the static maximum gape phase (MG-phase) was not an obligatory element of the ingestion and transport gape cycles of the European Pond Turtle. Our results show that the aquatic food uptake kinematics were rather uniform, which might indicate a feed-forward controlled motor program. In food transport cycles, our experimental specimens showed individual kinematical variations. In the European Pond Turtles terrestrial feeding seemed to be challenging. Recently it was reported that the adults of this species are able to fulfill the whole feeding process including food uptake, food transport, pharyngeal packing and swallowing on land. We tested whether subadult European Pond Turtles can feed on land as well. During our investigation we did not detect any of the subadult European Pond Turtles to attempt terrestrial food transport. Very rarely the turtles grasped food offered on land by their jaws, but dragged it immediately under water for further manipulation and swallowing.

**Key words:** testudinids, food uptake, food transport, suction, ontogenetic shift, high-speed video recording

## Introduction

The variations in movements of the feeding apparatus may rely on many factors, some of which are conditioned by the differences in the feeding medium, i.e. water vs air. Feeding in both media allows expanding the trophic spectrum (for overview see SCHWENK 2000a). However, the physical properties of water and air as feeding media (see LAUDER 1985a) demand different constructions of the feeding apparatus in aquatic and terrestrial tetrapods (REILLY & LAUDER 1990). Function and form of the feeding apparatus in chelonians vary dramatically between aquatic and terrestrial species (BRAMBLE 1973,

BRAMBLE & WAKE 1985, LAUDER 1985b, LEMELL et al. 2000, BEISSER et al. 2001). Underwater, most tetrapods catch prey by using “compensatory suction feeding” (sensu VAN DAMME & AERTS 1997), i.e. a combination of fast forward movement of the cranio-cervical complex known as “ram feeding” (see LAUDER & PRENDERGAST 1992, LIEM 1980, NORTON & BRAINERD 1993) and rapid expansion of the oropharyngeal cavity. The latter generates a negative pressure in the oropharyngeal cavity, which compensates the “bow wave” created by the fast forward movement of the head and causes water and

prey to rapidly flow into the mouth (VAN DAMME & AERTS 1997).

In turtles, the functional morphology of the feeding apparatus is not completely understood (for overview see NATCHEV et al. 2015a). The tongues of purely aquatic feeding turtles are small with no or poorly developed lingual papillae and oral glands (IWASAKI 1992, BEISSER et al. 1995, 2001, LEMELL et al. 2002), which provides hydrodynamic advantages. In contrast, terrestrial turtles have well-developed tongues studded with lingual papillae used for the terrestrial, lingual based feeding mechanism (BRAMBLE & WAKE 1985, WINOKUR 1988, WOCHESLÄNDER et al. 1999).

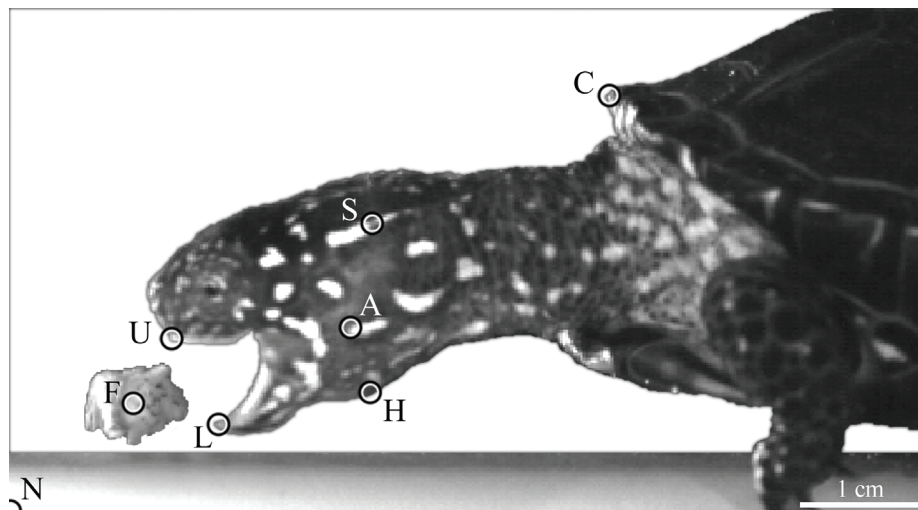
Compared with other tetrapods, detailed descriptions on feeding mechanisms in turtles are relatively scarce (for overview see SCHWENK 2000b, BELS et al. 2008, NATCHEV et al. 2009, 2011, 2015a). Terrestrial feeding in emydids was considered to have evolved independently from the two other groups of the superfamily Testudinoidea, namely the geoemydids and testudinids (SUMMERS et al. 1998, NATCHEV et al. 2009, 2015a). The feeding ecology of the emydid *Emys orbicularis* has been controversially reported to be purely aquatic (ERNST & BARBOUR 1989, STEPHENS & WIENS 2003, DROBENKOV 2014), or partly terrestrial, as some phases in the life history of the European Pond Turtle seem to be highly related to land habitats (for overview see FICETOLA & DE BERNARDI 2006). Some turtle species with predominantly aquatic lifestyle are able to grasp food on land, but are unable to fulfill transport cycles outside the water (WEISGRAM 1985a,b, HEISS et al. 2010). PRITCHARD (1979) reported different feeding media preferences between individuals in *E. orbicularis* and WOLF (2004) observed that the European Pond Turtle captures food outside water both in captivity and in the wild. It is important to note, however, that “food uptake” on land is not equivalent to “terrestrial feeding” as “food uptake” only comprises initial grasping of the food without intraoral transport or swallowing actions. Under laboratory conditions, adult European pond turtles are able to ingest, transport and swallow food on land (NATCHEV et al. 2015b). OTTONELLO et al. (2005) reported a very high percentage (>60%) of terrestrial insects in the diet of *E. orbicularis*, so it is possible that terrestrial feeding is an element of the natural behavioural repertoire in wild populations. Ontogenetical transitions in the feeding media preferences are reported for some aquatic turtle species (HEISS et al. 2009). Within the present study, we provide experiments to test: a) feeding kinematics under water, and b) whether subadult European

Pond Turtles feed on land under laboratory conditions. Using high-speed video recordings, we examine whether the feeding kinematic profiles reflect pure aquatic or semi-aquatic feeding ecology. We also search for possible variation in prey capture and intraoral transport movements within and between individuals to test whether movements are stereotypical – and therefore pre-programmed – or are modulated regularly due to behavioural plasticity.

## Materials and Methods

The distribution area of the European Pond Turtle, *E. orbicularis* (L., 1758), ranges from the Republic of Belarus south to Morocco, with a west-east distribution from the Portuguese Atlantic coastline to the Caspian Sea (ERNST & BARBOUR 1989, BONIN et al. 2006). The habitats include both slow-running waters with soft river beds, as well as stagnant waters. The use of terrestrial basking places and terrestrial migration routes points to a semi-aquatic lifestyle (STOJANOV et al. 2011). The European Pond Turtle is mainly carnivorous and feeds predominantly on aquatic and terrestrial invertebrates (BANNIKOV 1951, KOTENKO 2000, MITRUS & ZEMANEK 2000) but also hunts for amphibians and fish (STOJANOV et al. 2011). Older individuals were reported to be omnivorous (PRITCHARD 1979, ERNST & BARBOUR 1989, DALL’ANTONIA et al. 2001, FICETOLA & DE BERNARDI 2006). For the present study, we used five subadult individuals (straight carapace length: 46.8–59.9 mm; weight: 37.6–49.0 g). The captive-bred animals were purchased commercially and kept in a glass aqua-terrarium with a ground area of 120×50 cm (20% land and 80% water) with a 12 h dark/12 h light cycle. The water level was constant and kept at a depth of 15 cm. Accessible basking places and hiding shelters were offered. A UV light source was provided. The animals were fed with fish pieces, vegetables and turtle-food pellets. Animal care and treatment was in accordance with the Austrian National Protection of Animals Act.

To analyse aquatic feeding kinematics, three of the five specimens were filmed in lateral view using a Photron Fastcam-X 1024 PCI (Photron, Tokyo) digital high-speed camera at 500 fps. For illumination, two Dedocool COOLH tungsten light heads with 2×250 W (ECL), supplied by a Dedocool COOLT3 transformer control unit (DedoWeigert Film GmbH; Munich, GER) were used. The animals were positioned in a glass aquarium (19×7×19 cm) with a reference grid (1×1 cm) in the background and a water level of 15 cm. Fish pieces (in size approximately



**Fig. 1.** Landmarks used for kinematic analysis of the aquatic feeding cycles in *E. orbicularis*. A – ventral margin of tympanum (jaw articulation); C – anterior tip of carapace; F – estimated centre of mass of feeding items; H – basis of the ceratobranchiale II on hyoid; L – anterior tip of lower jaw; N – point “zero” on measurement board; S – dorsal margin of tympanum (dorsal-most point of squamosal); U – anterior tip of upper jaw

half of the length of the upper jaw of the turtles) were offered on the bottom of the glass aquarium, directly in front of the animals.

A total of 18 films (six films for each of three specimens) were digitally analysed using the SIMI-MatchiX software (SIMI Reality Motion Systems, Unterschleisheim, Germany). The following anatomically relevant landmarks were selected (Fig. 1): A – the position of the mandible jaw joint; C – the anterior tip of the carapace; F – estimated centre of gravity mass of the food item; H – basis of the second hyoid horns (Ceratobranchiale II); L – tip of the lower jaw; N – point zero of the screen (point 0); S – dorsal tip of the tympanum; U – tip of the upper jaw. On the basis of the landmarks' displacement along the x-y coordinates we calculated the distance between the tips of the upper and lower jaw (distance between points U and point L), the rostro-caudal head movements (distance between point C and point S), the movements of the hyoid (distance between point A and point H), and the movement of the food item (distance between point F and zero-point N).

To examine terrestrial feeding behaviour, we used all five subadult specimens. The housing aqua-terrarium was adjusted by a transparent platform (50×25 cm) 5 cm above the water level. On this platform, we offered food (always 6 pellets), which was permanently visible for the turtles. This way we attempted to simulate terrestrial feeding conditions. We provided access from the water to the platform by a slant climbing plate with furrows to facilitate the access to the offered food. Food pellets were removed when the platform was not controlled by the

team or during the night. The experiment was performed for 92 days.

A multivariate analysis of variance (MANOVA) was performed to test for differences between (i) the feeding modes ingestion and transport and (ii) between individuals in the feeding modes ingestion and transport. The model residuals (MANOVA residuals) were tested for normal distribution by the K-S-test and were normally distributed for each variable. The nine variables used to compare feeding kinematic patterns are listed in Table 1. All statistical tests were performed using SPSS 11.5 (IBM, Chicago, USA) software ( $\alpha = 0.05$ ).

## Results

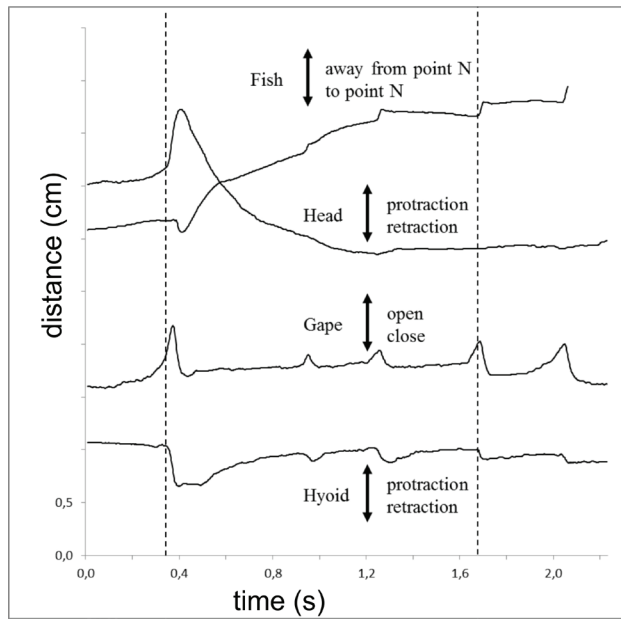
From a total of 18 aquatic feeding sequences, we obtained 18 food uptake cycles and 59 transport cycles (Table 1). Every sequence included one ingestion cycle, and one to seven (average  $3.3 \pm 1.7$  per film sequence) transport cycles (Fig. 2). Food uptakes kinematics were similar for all three individuals, so we averaged these data. Transport cycles were executed quite variably for each individual, so they were analysed separately.

For prey capture, the hyoid depression started  $17 \pm 8$  ms prior to reaching peak gape (Figs. 2, 3). We clearly detected that, after hyoid retraction, the fish piece moved toward the predator (Fig. 2). In only 11.1% of the prey capture cycles, the peak gape showed a plateau of  $10 \pm 3$  ms. In the other cases the jaw closing began immediately after reaching the maximum gape. In all 18 sequences the prey was fixed between the jaws. After jaw closing, the hyoid protracted again

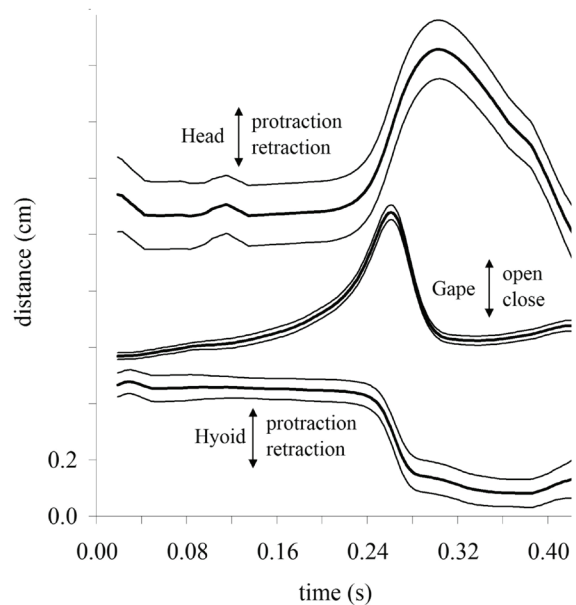
**Table 1.** Descriptive statistics of kinematic variables of food ingestion and transport and subsequent ANOVAs testing for effects of individual and feeding mode (ingestion vs. transport). Variables used for MANOVA:  $t_{FO}$  fast opening,  $t_p$  maximum gape plateau duration,  $t_{FC}$  fast jaw closing duration,  $t_{CD}$  total cycle duration,  $t_{HD}$  hyoid depression duration,  $t_{HFOB}$  hyoid depression delay to fast opening begin,  $V_{FO}$  fast jaw opening velocity,  $V_{FC}$  fast jaw closing velocity,  $V_{HR}$  hyoid retraction velocity

variables	Ingestion				Transport				F-ratio <sup>3</sup>	P-ratio <sup>3</sup>	
	animal 1 (n=8)	animal 2 (n=6)	animal 3 (n=4)	P-ratio <sup>1</sup>	animal 1 (n=23)	animal 2 (n=15)	animal 3 (n=21)	F-ratio <sup>2</sup>			P-ratio <sup>2</sup>
$t_{FO}$ (s)	0.066 ± 0.036	0.060 ± 0.023	0.052 ± 0.017	$F_{2,71} = -0.447$	0.061 ± 0.029	0.029 ± 0.007	0.052 ± 0.025	$F_{2,71} = 7.474$	0.001*	$F_{1,71} = 2.996$	0.88
$t_p$ (s)	0.002 ± 0.004	0.000 ± 0.000	0.002 ± 0.004	$F_{2,71} = -0.129$	0.007 ± 0.011	0.000 ± 0.000	0.001 ± 0.005	$F_{2,71} = 7.177$	0.001*	$F_{1,71} = 0.765$	0.385
$t_{FC}$ (s)	0.042 ± 0.01	0.051 ± 0.013	0.033 ± 0.008	$F_{2,71} = -0.881$	0.069 ± 0.032	0.046 ± 0.010	0.042 ± 0.012	$F_{2,71} = 11.43$	0.001*	$F_{1,71} = 4.006$	0.49*
$t_{CD}$ (s)	0.110 ± 0.037	0.109 ± 0.029	0.087 ± 0.020	$F_{2,71} = -0.700$	0.138 ± 0.047	0.075 ± 0.012	0.095 ± 0.031	$F_{2,71} = 16.88$	<0.001*	$F_{1,71} = 0.007$	0.932
$t_{HD}$ (s)	0.044 ± 0.017	0.036 ± 0.009	0.038 ± 0.010	$F_{2,71} = -0.162$	0.056 ± 0.017	0.056 ± 0.025	0.037 ± 0.015	$F_{2,71} = 0.823$	0.443	$F_{1,71} = 0.554$	0.459
$t_{HFOB}$ (s)	-0.049 ± 0.040	-0.042 ± 0.029	-0.035 ± 0.020	$F_{2,71} = -0.307$	-0.029 ± 0.025	-0.006 ± 0.010	-0.026 ± 0.043	$F_{2,71} = 2.737$	0.072	$F_{1,71} = 5.999$	0.017*
$V_{FO}$ (cm/s)	6.906 ± 2.523	5.876 ± 0.610	5.765 ± 1.508	$F_{2,71} = -0.364$	4.124 ± 2.260	6.782 ± 4.461	2.885 ± 1.731	$F_{2,71} = 9.504$	<0.001*	$F_{1,71} = 4.552$	0.036*
$V_{FC}$ (cm/s)	11.746 ± 3.268	10.023 ± 1.381	12.636 ± 6.580	$F_{2,71} = -0.929$	5.031 ± 3.119	6.524 ± 3.663	5.554 ± 2.097	$F_{2,71} = 1.023$	0.365	$F_{1,71} = 43.133$	<0.001*
$V_{HR}$ (cm/s)	9.970 ± 3.784	7.390 ± 1.293	7.950 ± 1.861	$F_{2,71} = 1.837$	4.499 ± 2.758	6.382 ± 4.473	3.491 ± 1.847	$F_{2,71} = 4.08$	0.021*	$F_{1,71} = 10.206$	0.002*

\*Significant differences ( $\alpha=0.05$ ) among individuals in the ingestion-phase ( $P^1$ ), among individuals in the transport phase ( $P^2$ ) and between ingestion and transport-phase ( $P^3$ )



**Fig. 2.** Representative kinematic profile of aquatic feeding event in *E. orbicularis*, including one prey capture and four prey transport cycles. Sequences were captured at 500 fps. The first (left) vertical line shows the beginning of the hyoid depression at prey capture time synchronised with the head protraction. The second (right) vertical line shows the beginning of the hyoid retraction at prey transport together with the beginning of the fish movement

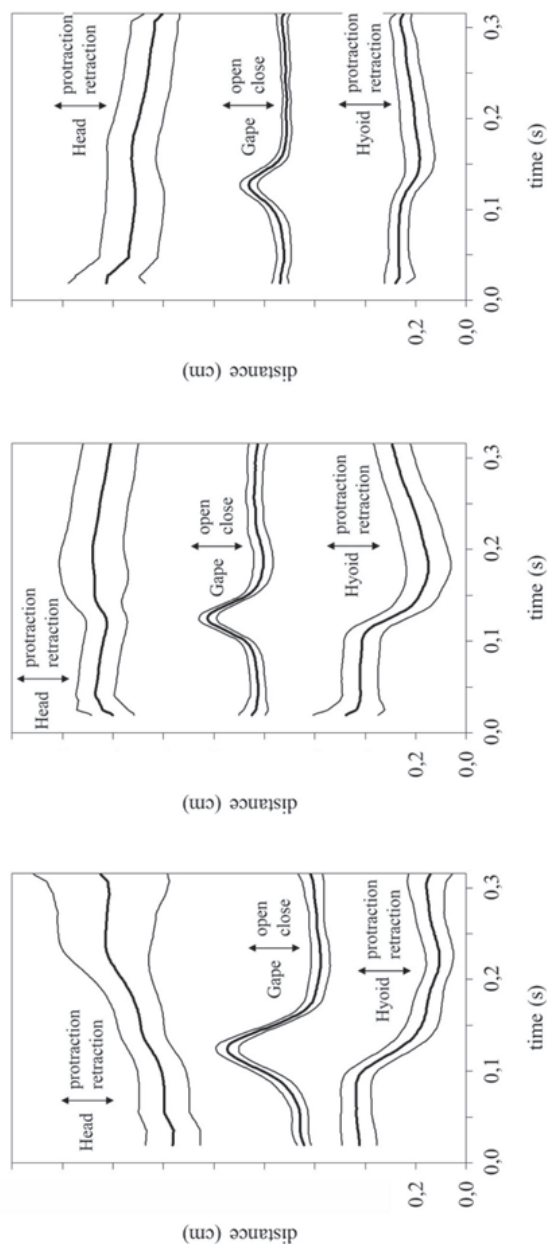


**Fig. 3.** Mean and standard error in the kinematic patterns of the elements of the feeding apparatus in food uptake cycles, combined for all three specimens

and the swallowed water visibly streamed out through the small jaw-slit. When the hyoid reached its most antero-dorsal position, the prey capture was completed and the transport cycles followed.

In some transport cycles, the peak gape showed





**Fig. 4.** Mean and standard error in the kinematic patterns of the elements of the feeding apparatus in food transport cycles, separate for all three specimens

a plateau (individual 1: 8 of 23 transport cycles, with an average of  $21 \pm 6$  ms; ind. 2: 0 of 15; ind. 3: 1 of 21, lasting 22 ms). Similar to the prey capture cycle, the hyoid depression started before the jaws reached their maximum gape (Fig. 4). During the transport cycles (1–7 per food item), the tongue contacted the prey during jaw opening.

The hyoid depression was faster in prey capture ( $0.079 \pm 0.038$  m/s) than in prey transports (individual 1:  $4.499 \pm 2.758$  cm/s; ind. 2:  $6.679 \pm 4.485$  cm/s; ind. 3:  $3.277 \pm 1.934$  cm/s). In all sequences, prey capture was accompanied by neck extension towards the fish but not all prey transport cycles included head

protraction (individual 1: 9 of 23; ind. 2: 10 of 15; ind. 3: 4 of 21) (Figs. 2, 3, 4).

The MANOVA revealed significant differences between ingestion and transport modes (Wilk's lambda  $F_{8,64} = 8.776$ ,  $P < 0.001$ ) and significant differences between individuals in the transport mode (Wilk's lambda  $F_{16,128} = 5.064$ ,  $P < 0.001$ ), but not between individuals in the ingestion mode (Wilk's lambda  $F_{16,128} = 0.919$ ,  $P = 0.549$ ). The subsequent series of ANOVAs showed that the significant difference between ingestion and transport modes was based on significant differences between five out of the nine variables tested while the significant difference between individuals in the transport mode was based on significant differences between six out of the nine variables tested (Table 1).

During the period of the experiments designed to investigate the terrestrial feeding behaviour in subadult *E. orbicularis*, we were not able to observe or film a whole feeding event (ingestion plus transport) on the feeding platform. All turtles fed readily when the food was offered in water, but were extraordinary cautious when food was offered on land. Only two of the five specimens were observed to take up food on the platform. One of the specimens executed six and the other one two food uptakes. In all eight events, the turtles climbed slowly on the platform, then grabbed a pellet with the jaws after several attempts. The turtles did not grasp the food items from above but twisted their necks to successfully bite on the pellets. This rotation of the head impeded filming in the lateral plane. After the food was fixed between the jaws, the turtles rushed toward the water and jumped over the edge of the platform. Food transport and swallowing were executed under water.

## Discussion

Turtles are amongst the oldest living amniotes and span the range from fully aquatic to fully terrestrial species, having consequently evolved adaptations to different trophic niches (see PRITCHARD 1979, BONIN et al. 2006, ORENSTEIN 2012). While terrestrial turtles usually are omnivorous to herbivorous and exhibit slow feeding movements, some aquatic turtles are highly specialized predators and rely on fast and tightly coordinated movements of the feeding apparatus to capture prey (for overview see LEMELL et al. 2002, NATCHEV et al. 2015a). In predatory vertebrates, the execution of fast aquatic feeding strikes requires firm coordination between the locomotor, sensory and feeding apparatus (WAINWRIGHT et al. 2007) – once prey capture is initiated there is little space for further kinematic modulation. This is

probably also true for the extremely fast striking turtles such as *Chelydra serpentina* L., 1758 (LAUDER & PRENDERGAST 1992), *Chelodina longicollis* Shaw, 1794 (VAN DAMME & AERTS 1997) or *Chelus fimbriatus* Schneider, 1783 (LEMELL et al. 2002), which are able to catch elusive prey. Little is known concerning the level of uniformity in the execution of feeding kinematics in less specialized, more opportunistic species with a wider trophic spectrum (NATCHEV et al. 2009, 2011). STAYTON (2011) studied the food uptake kinematics in eight emydid turtles and showed clear differences between aquatic and terrestrial bitings; furthermore, he emphasized the importance of the capability of behavioural plasticity in acquiring new niches.

*Emys orbicularis* is a species with a broad trophic spectrum, so high plasticity of the feeding kinematics could be expected. Our results pointed to a more complex conclusion. Actually, the kinematic patterns in underwater food transport cycles are rather variable between the investigated individuals. Similar results were reported for terrestrial feeding in subadults of *Manouria emys emys* Schlegel & Müller, 1844 (NATCHEV et al. 2015a). In contrast to the kinematics of the transport cycles in *E. orbicularis*, the three individuals tested in that study showed great similarities in execution of underwater food uptake (Table 1, Fig. 3). The mechanism of the food uptake can be described as typical “compensatory suction” (sensu VAN DAMME & AERTS 1997). The head protraction and the hyoid depression are highly synchronised during the food grasping (Figs. 2, 3). This synchronisation is apparently very important for the successful execution of the aquatic food uptake. The motor program seems to fit to the “feed forward” type (see DEBAN et al. 2001, DEBAN & DICKE 2004) as all movements were performed completely identically in all of the three experimental specimens (Fig. 4). The high degree of uniformity of the kinematical patterns during aquatic prey capture is usually found in species that are able to generate significant suction flow and execute the capture event in very short time (VAN DAMME & AERTS 1997, LEMELL et al. 2002). This is not the case in *E. orbicularis*. The graphic representing the prey movements indicates that initially the food item is pushed away by the bow wave created by the approaching head and gaping mouth of the turtle (Fig. 2). The movement of the food towards the zero point of the screen starts shortly prior to reaching peak gape during the fast neck extension. In this moment the hyoid retraction has already been initiated. The fact that the food is pushed away by the turtle’s protracting head despite the hyoid depression, indicates that the

abrupt oro-pharyngeal expansion cannot fully compensate the bow wave. We propose that the uniformity of the food uptake movements in the subadult *E. orbicularis* is constrained by the morphology of the turtle’s prey capture apparatus. The species has a hyoid construction that does not allow generation of strong suction forces – turtles, which are specialized in suction feeding, possess bony hyoid bodies and horns. In *E. orbicularis*, the hyoid complex is mainly cartilaginous (see BOJANUS 1819, NATCHEV et al. 2015b). We suggest that European Pond Turtles have to take up food in a stereotype manner, because the feeding apparatus is efficient only in the execution of one particular, precisely coordinated set of feeding movements. The low degree of variation may constrain the feeding performance and the ability of *E. orbicularis* to feed on elusive prey. On the other hand, the bendable hyoid may be advantageous for the European Pond Turtle – this design allows it to perform precise food manipulation and multidirectional food transport. Our results indicate that the transport/manipulation kinematics are under complex feedback control. The construction of the hyoid complex may negatively impact the suction feeding performance of the species, but it allows the turtle to transport food by applying complex combinations of “compensatory” and “inertial suction” mechanisms (Table 1, Figs. 2,4). During transport and manipulation, the food is already within the margins of the mouth. In *E. orbicularis*, the suction forces work apparently more efficiently on food items that are already inside the oropharynx. The motor program of the transport cycle can be more variable and fine-tuned under feedback control for every single feeding situation.

Initial measurements based on high-speed video recordings indicate that adult European Pond Turtles utilise the same set of movements when executing terrestrial and aquatic food transports (NATCHEV et al. 2015b). Unfortunately, we were not able to confirm that observation for subadults. Anatomical and histological investigation of the oropharynx as well as further ethological studies will provide information whether there is a clear ontogenetic shift in the potential of *E. orbicularis* to exploit terrestrial food resources.

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