

## RESEARCH ARTICLE

# The effect of food properties on grasping and manipulation in the aquatic frog *Xenopus laevis*

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## ABSTRACT

The ability to grasp an object is fundamental from an evolutionary perspective. Involved in many daily activities, grasping has been extensively studied in primates and other mammals. Yet other groups of tetrapods, including anurans, have also evolved significant forelimb prehensile capacities that are often thought to have originated in an arboreal context. In addition, grasping is also observed in aquatic species. But how aquatic frogs use their forelimbs to capture and manipulate prey remains largely unknown. The aim of this study is to explore how the grasping and manipulation of food items in aquatic frogs is impacted by food properties such as size and mobility. To do so, we used the aquatic frog *Xenopus laevis* and quantified the use of the hands and fingers while processing mobile and stationary prey of different sizes (small, intermediate and large). Our results show that *X. laevis* is able to individualize the digits and that the mobility and the length of the prey significantly influence the kind of grasping pattern used. Grasping abilities are thus not specific to terrestrial or arboreal species. These results illustrate how prey properties impact grasping and manipulation strategies in an aquatic frog and shed further light on the ecological contexts that may have given rise to the origin of grasping in frogs.

**KEY WORDS:** Prehension, Manipulation, Prey properties, Anurans, Digits, Dexterity, Hand

## INTRODUCTION

The ability to grasp an object with an appendage is fundamental from an evolutionary perspective (Sustaita et al., 2013). It can be accomplished by the hand, foot, tail, trunk, tongue, teeth or other parts of the body (Mackenzie and Iberall, 1994). Involved in many daily activities, hand grasping has been extensively studied in primates, which are characterized by the ability to individualize their fingers and thus able to perform complex grasping and manipulation tasks (e.g. Christel, 1993; Jones-Engel and Bard, 1996; Christel et al., 1998; Christel and Billard, 2002; Crast et al., 2009; Pouydebat et al., 2008, 2009, 2011; Peckre et al., 2016). Anurans have also evolved significant prehensile abilities that in some cases involve individualization of the fingers (e.g. Manzano et al., 2008; Abdala and Diogo, 2010). Whereas frogs typically transfer small prey to the esophagus with the tongue or jaws, the hands play an important role in the manipulation of larger prey (Anderson and Nishikawa, 1996; Valdez and Nishikawa, 1997).

However, in contrast to studies on the role of the tongue and jaws during prey capture (Nishikawa, 1999, 2000; Monroy and Nishikawa, 2011), studies on the use of the forelimbs during feeding are rather scarce (Gray et al., 1997).

Previous studies on anurans have identified five distinct behavioral patterns that involve the use of the forelimbs: (1) scooping, involving the use of the back of the hand to push prey into the mouth as observed for *Xenopus laevis* Daudin 1802 and *Rana pipiens* (Avila and Frye, 1977, 1978; Comer and Grobstein, 1981; Gray et al., 1997); (2) wiping, involving the use of the palm of the hand to push prey protruding laterally from the mouth as observed in *X. laevis*, *R. pipiens* and *Hymenochirus boettgeri* (Sokol, 1969; Avila and Frye, 1978; Comer and Grobstein, 1981; Gray et al., 1997); (3) prey stretching, involving the grasping of one end of the prey by the hands while the other end is pulled upward by the jaws (Gray et al., 1997); (4) grasping, involving the wrapping of the fingers around the prey (Gray et al., 1997); and (5) finally, hand grasping was observed for several species, involving grasping motions by the hands instead of the tongue to capture and transport prey from the external environment into the mouth (Gray et al., 1997).

The goal of the present study is to quantify the use of the hands during prey grasping and manipulation in the aquatic frog *X. laevis*. Moreover, we test whether and how food properties modify the use of the hands. As has been described for primates (Pouydebat et al., 2009, 2014; Toussaint et al., 2013, 2015), the mobility and the size of a prey item may affect the grasping and manipulation strategies used (e.g. the use of two hands versus one hand, and which fingers are involved in grasping). Specifically, we predict that larger prey will involve an increased use of the hands during grasping as observed in many other taxa (Sustaita et al., 2013). We also predict that mobile prey will induce the use of the hands more as observed in mouse lemurs, for example (Toussaint et al., 2013). Finally, we also explore whether this species is able to individualize the fingers as observed in some marsupials, carnivores and primates (Sustaita et al., 2013).

## MATERIALS AND METHODS

### Animals

*Xenopus laevis* were housed at the laboratory [UMR 7179, Muséum National d'Histoire Naturelle (MNHN), Paris, France] in groups of three to eight individuals in aquaria (60×30×30 cm) with the temperature set at 23°C, which is close to the preferred and optimal temperature of *Xenopus* frogs (Casterlin and Reynolds, 1980; Miller, 1982). Frogs were fed every other day with beef heart, earthworms or mosquito larvae *ad libitum*. All individuals were pit-tagged (NONATEC, Rodange, Luxembourg) before the onset of the experiments, allowing unambiguous identification of each individual. A total of 10 individuals (five males: snout–vent length 70.3±3.5 mm, hand+finger length: 16.1±1.7 mm; five females: snout–vent length 83.9±9.3 mm, hand+finger length: 17.1±2.1 mm) were included in the present study. All experiments were

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approved by the institutional ethics committee at the MNHN (Comité Cuvier no. 68-25).

### Video recordings

Video cameras were placed around the experimental aquarium in order to obtain lateral and ventral views of *X. laevis* capturing and manipulating prey. Two Prosilica GE680 640×480 cameras (Allied Vision Technologies, Stadtroda, Germany) were used to film at 200 frames s<sup>-1</sup>. Lighting was provided by two spotlights (PAR-400S-230; Kino Flo Lighting Systems, Burbank, CA, USA) placed in front of the experimental aquarium. Animals were placed in the filming tank (100×20×18 cm, filled with 10 cm of water and maintained at 24°C) and fed while being filmed.

### Prey types

To test the various techniques of capture used by *X. laevis*, six types of prey were selected. They were classified according to two parameters: size (large, medium or small) and mobility (mobile or immobile). The size of the prey was determined relative to the size of the hand of the frogs. Small prey were less than half of the length of the hand (8 mm), medium prey were double the size of the hand (32 mm) and large prey were approximately five times the size of the hand (80 mm). The small mobile prey were honeycomb moth larvae (*Galleria mellonella*). The medium and large mobile prey were live mosquito larvae or earthworms (*Chironomus plumosus* or *Dendrobaena veneta*). The small immobile prey were dead mosquito larvae (*Chironomus plumosus*) and the medium and large immobile prey were dead earthworms (*Dendrobaena veneta*) cut to the appropriate size. The types of prey were all vermiform to avoid a possible bias for the recognition of a particular shape of prey. A total of 10 sequences were recorded for each individual and for each prey type, resulting in a total of 600 videos analyzed.

### Video analyses

The behavior used to grasp a food item was analyzed. During the video analyses, the fingers used to grasp the prey were noted: between fingers I and II, II and III, and III and IV. The hand preference of the individuals (right versus left, or the use of both hands) was also analysed. These observations indicated that all of these patterns were preceded or followed by a positioning of the hands on the mouth to prevent the prey from escaping from the mouth after capture. Two other patterns observed here but not

previously described in the literature were added: (1) ‘pushing’ and (2) ‘shredding’. ‘Pushing’ involves a movement of the hand towards the mouth but without it touching the prey and involving body movements of the frog. This behavior is different from suction, where no movement of the hand towards the mouth is observed and where the body typically remains motionless. ‘Shredding’ involves the use of the hind limbs to tear the biggest prey into smaller pieces.

### Statistical analyses

We first calculated the proportions of the different behaviors used during prey grasping and manipulation. The proportions were then arcsin-transformed to render the data normal (Sokal and Rohlf, 2012). A factor analysis with rotation (varimax) was then used to reduce the dimensionality of the data set. Five main axes explaining 73.6% of the variability were retained and used as input for the subsequent analyses. We first ran a MANCOVA with prey size, mobility and sex as fixed factors and frog body mass and prey handling behavior as covariables. However, as the effects of sex (Wilks’ lambda=0.84,  $F_{10,84}=0.74$ ,  $P=0.68$ ) and body mass (Wilks’ lambda=0.87,  $F_{5,42}=1.22$ ,  $P=0.32$ ) were not significant they were removed from the model. A MANOVA with prey size and prey mobility as fixed effects was thus used to test whether size and mobility impacted the prey handling behavior. Given that the interaction between size and mobility was significant (Wilks’ lambda=0.49,  $F_{10,100}=4.32$ ,  $P<0.001$ ), we ran tests (MANOVA) for the effect of mobility separately for the different size classes, and tests for the effect of size separately for both mobile and immobile prey. All MANOVAs were coupled to univariate ANOVAs to test which factors differed from one another. Finally, Bonferroni *post hoc* tests were used to test which size classes were different from one another. All statistical analyses were performed using IBM SPSS V.23 (IBM, Armonk, NY, USA).

### RESULTS

In the following description of the observed behaviors, all behaviors are noted relative to the total number of grasping movements observed. All patterns described in the literature (Gray et al., 1997) except scooping were observed for *X. laevis* (see Fig. 1 for examples). However, shredding was only observed when manipulating large prey. On average, the *X. laevis* included in our study needed 1.2 attempts per prey item before it could be captured. Our observations showed that the left hand is preferentially used

**Table 1. Proportions of the different behaviors observed as well as the average number of prey capture attempts needed to capture different types of prey**

	Immobile			Mobile		
	Large	Medium	Small	Large	Medium	Small
Suction	0.11±0.04	0.22±0.08	0.31±0.09	0.13±0.05	0.18±0.05	0.15±0.08
Pushing	0.14±0.06	0.32±0.11	0.59±0.15	0.14±0.07	0.35±0.15	0.55±0.19
Wiping	0.69±0.16	0.40±0.13	0.10±0.06	0.55±0.13	0.42±0.14	0.30±0.17
Stretching	0.07±0.07	0.02±0.03	0.00±0.00	0.18±0.12	0.06±0.06	0.02±0.03
Shredding	0.0008±0.003	0.0048±0.01	0.00±0.00	0.013±0.01	0.0009±0.003	0.00±0.00
II–III	0.22±0.16	0.17±0.25	0.17±0.47	0.27±0.15	0.20±0.19	0.60±0.69
III–IV	0.50±0.40	0.50±0.44	0.48±0.68	0.35±0.25	0.34±0.27	0.21±0.51
IV–V	0.33±0.44	0.31±0.27	0.48±0.68	0.19±0.19	0.24±0.20	0.44±0.63
All fingers	0.06±0.10	0.10±0.14	0.02±0.05	0.21±0.26	0.05±0.08	0.05±0.17
Right	0.35±0.11	0.35±0.06	0.28±0.12	0.33±0.07	0.36±0.09	0.37±0.10
Left	0.33±0.07	0.41±0.11	0.45±0.14	0.39±0.08	0.41±0.11	0.49±0.09
Bimanual	0.32±0.09	0.25±0.13	0.27±0.16	0.28±0.08	0.23±0.11	0.15±0.09
No. of attempts	1.14±0.13	1.18±0.18	1.20±0.16	1.29±0.23	1.12±0.14	1.32±0.18

Table entries are mean±s.d. proportions. No. of attempts is the mean±s.d. number of attempts. Pushing refers to the behavior where the frog appears to push prey towards the mouth but without touching it.

(41.4%), followed by the right hand (33.8%) and both hands (24.8%). The fingers that were most often used to grasp prey were fingers II–III (37.0%), fingers III–IV (30.6%) and finally fingers I–II (25.4%). The use of all fingers during grasping was rather uncommon (7%). Of the different behaviors observed, wiping was most common (41.3%), followed by pushing (34.8%) and suction (18.3%). Stretching (5.3%) and shredding (0.3%) were only occasionally used by *X. laevis*. A summary of the behaviors observed is presented in Table 1.

The factor analysis retained five factors jointly explaining 73.6% of the overall variability in the data set (Table 2). The first axis was strongly positively determined by the proportion of suction and the proportion of pushing used, and negatively by the proportion of wiping used (Table 2, Fig. 2). The second axis was positively determined by the proportions of stretching and shredding behaviors used (Table 2, Fig. 2). Whereas the third axis was positively determined by the use of fingers II–III and the use of the right hand, the fourth axis was positively determined by the use of the left hand and negatively by the use of both hands (bimanual grasping; Table 2). The fifth and final axis was negatively determined by the use of fingers II–III during grasping (Table 2).

The MANOVA performed on the factor scores showed significant effects of prey mobility (Wilks' lambda=0.66,  $F_{5,50}=5.21$ ,  $P=0.001$ ), prey size (Wilks' lambda=0.21,  $F_{10,100}=11.87$ ,  $P<0.001$ ) as well as the interaction between size and mobility (Wilks' lambda=0.49,  $F_{10,100}=4.32$ ,  $P<0.001$ ). Subsequent univariate ANOVAs showed that effects of mobility were significant on axes 1, 2, 3 and 4 (Table 3, Fig. 2). However, effects of prey size were significant only on axes 1 and 2 (Fig. 2). Interaction effects were also only significant on axes 1 and 2 (Fig. 2).

Given the significant interaction effect, we next tested for differences between size classes for immobile prey, which were significant (Wilks' lambda=0.09,  $F_{10,46}=10.65$ ,  $P<0.001$ ). Univariate ANOVAs further showed that this effect was significant for axis 1 only ( $F_{2,27}=99.64$ ,  $P<0.001$ ) with all three groups being significantly different from one another as indicated by the *post hoc* tests (all  $P<0.001$ ). Inspection of the means showed that large prey had low scores on this axis, intermediate sized prey had intermediate scores and small prey had high scores, suggesting that small immobile prey are captured using suction and pushing whereas large immobile prey are associated with wiping behavior. When testing for effects of size on mobile prey, the MANOVA was also significant (Wilks' lambda=0.23,  $F_{10,46}=5.02$ ,  $P<0.001$ ). However, the univariate ANOVAs now showed significant effects

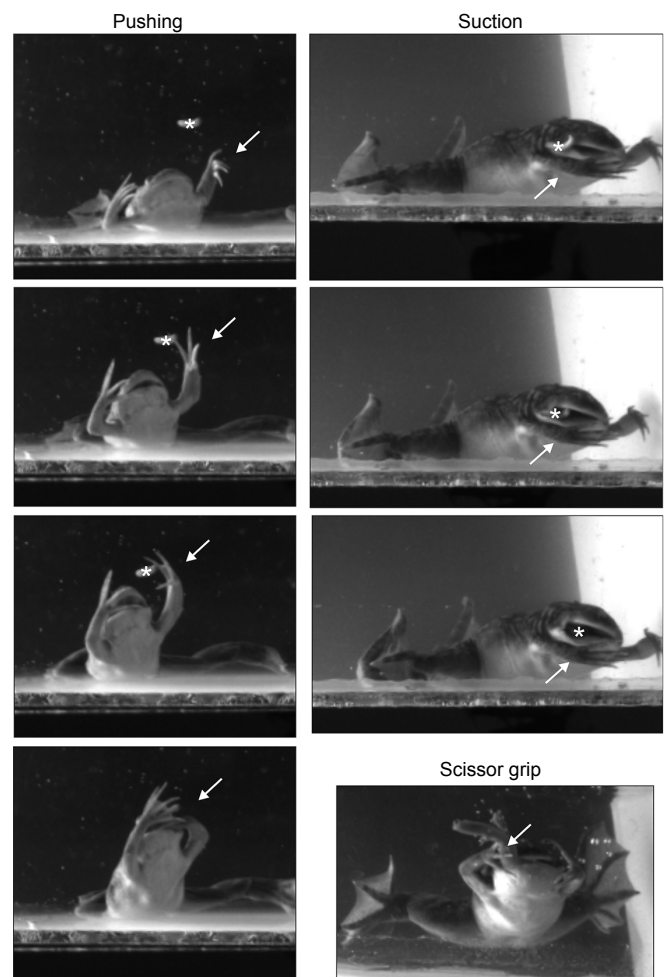
on axes 1 ( $F_{2,27}=5.79$ ,  $P=0.008$ ), 2 ( $F_{2,27}=8.07$ ,  $P=0.002$ ), 4 ( $F_{2,27}=3.89$ ,  $P=0.033$ ) and 5 ( $F_{2,27}=3.79$ ,  $P=0.035$ ). *Post hoc* tests showed that differences were significant between large and small prey only on axis 1, with small prey having high scores, as observed for immobile prey. On the second axis, large prey were different from both small and intermediate sized prey, with large prey having large scores and thus showing more stretching and shredding behavior. The fourth axis again discriminated only between large and small prey, with small prey having high scores, suggesting that the capture of small mobile prey is associated with the use of the left hand and a decrease in the use of both hands. The fifth axis finally discriminated specifically between small and intermediate sized prey, with small prey having large scores and thus a decrease of the use of fingers III–IV during grasping in contrast to intermediate sized prey, where fingers III–IV are preferentially used.

When testing for effects of mobility for large prey only, no significant effects were observed (Wilks' lambda=0.51,  $F_{5,14}=2.73$ ,  $P=0.06$ ). Similarly, for prey of intermediate size, no effects of mobility were detected (Wilks' lambda=0.87,  $F_{5,14}=0.42$ ,  $P=0.83$ ). However, for small prey, significant effects of mobility were observed (Wilks' lambda=0.35,  $F_{5,14}=5.24$ ,  $P=0.006$ ). Subsequent

**Table 2. Factor loading of the original behavioral variables on the first five axes after varimax rotation**

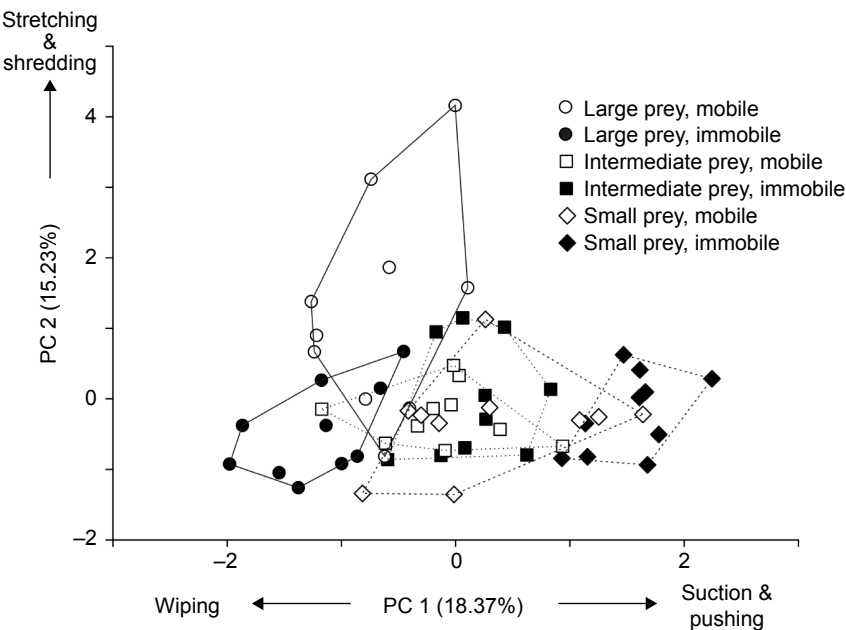
	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
% Variation	18.37	15.23	13.98	13.21	12.86
Suction	<b>0.73</b>	−0.21	−0.14	−0.12	−0.08
Pushing	<b>0.82</b>	−0.29	0.06	0.20	0.08
Wiping	− <b>0.94</b>	0.02	−0.01	−0.15	−0.11
Stretching	−0.42	<b>0.69</b>	0.02	−0.07	0.02
Shredding	−0.24	<b>0.72</b>	−0.07	−0.14	−0.07
Digits I–II	0.06	0.003	<b>0.72</b>	−0.04	0.46
Digits II–III	−0.003	0.07	0.07	0.08	− <b>0.87</b>
Digits III–IV	0.002	−0.45	−0.63	0.10	0.42
All digits	−0.02	<b>0.72</b>	−0.08	0.11	0.22
Right hand	−0.13	−0.25	<b>0.79</b>	0.12	−0.02
Left hand	0.22	0.05	−0.26	<b>0.89</b>	0.01
Bimanual	−0.08	0.14	−0.39	− <b>0.88</b>	0.14
Number of attempts	0.06	0.24	0.15	0.08	0.66

Bold values indicate high loadings (over 0.7) on each axis.



**Fig. 1. Video images illustrating three of the behaviors observed.** Note how during pushing, the hand (indicated by an arrow) is moved towards the prey (indicated by an asterisk) and subsequently towards the mouth but without touching the prey. During suction the hands do not move. On the bottom right is illustrated a scissor grip, where the earthworm is grasped between the fingers and brought to the mouth.





**Fig. 2. Results of a principal component analysis illustrating the different behaviors used for prey of different sizes and mobility.** The proportion of variance explained by each axis is illustrated, as well as the variables loading most strongly on each axis. The first axis mainly discriminates between prey of different sizes. Small prey (diamonds) are associated with the use of suction and pushing, whereas large prey (circles) and especially large immobile prey involve extensive wiping. The second axis discriminates between mobile large prey (open circles) that involve lots of prey stretching and shredding in contrast to immobile prey.

univariate ANOVAs showed that the effect was significant on the first axis only ( $F_{1,18}=7.72$ ,  $P<0.001$ ), with immobile small prey showing larger scores and thus being associated with more suction and pushing and less wiping.

DISCUSSION

Our results show that when prey are motionless, suction and pushing are used for capturing small prey and wiping is associated with large prey. Intermediate sized prey involve the use of both suction and wiping. However, when prey are mobile, the patterns depend on the size of the prey. Indeed, suction, pushing and wiping, as well as the involvement of the left hand or both hands at the same time are used differently for large versus small prey. Moreover, to grasp mobile prey of intermediate size, fingers II–III were used significantly more frequently. These fingers are the longest fingers and may allow for a more secure grip. Finally, stretching, shredding, and bimanual

behaviors are not used in the same way for the three size categories. Our study thus shows that *X. laevis* uses many different behaviors and prey manipulation strategies, which leads to an overall complex prey capture behavior. Although anurans are not known for their prehensile skills, they are capable of using their hands and fingers in different ways in order to adapt their movements to the properties of the prey. The morphology of the forelimb in *X. laevis* is very different from that of other taxa, showing highly developed manual prehension skills such as those in primates. Yet, despite these anatomical differences, they execute complex capture movements adapted to prey properties. Similar to humans and great apes (Christel, 1993; Christel et al., 1998; Crast et al., 2009; Pouydebat et al., 2011; Bardo et al., 2016), *X. laevis* is capable of prehension movements involving the fingers despite the absence of an opposable thumb on the hand. It is interesting to note that this species seems to have prehensile capacities that are even more complex than those observed in some primates, including some strepsirrhines (Reghem et al., 2011; Toussaint et al., 2013; Peckre et al., 2016) or platyrrhines (E.P., personal observation), capuchin monkeys excluded (Christel and Fragaszy, 2000; Spinozzi et al., 2004). Moreover, *X. laevis* presents a greater capacity for finger individualization compared with most other tetrapods (Sustaita et al., 2013).

Despite having been reported in the literature for *X. laevis* (Gray et al., 1997), scooping was not observed in our study. However, a previously undescribed pattern was observed: the use of the hand to ‘push’ the prey towards the mouth. Based on our videos we were unable to determine whether during this behavior the frog induces a flow of water by moving the hand towards the mouth or whether the frog performs a ram-like behavior where the body moves towards the prey and overtakes it. In the latter case, the movement of the hands towards the mouth may prevent the prey from being pushed away by the movement of the frog towards it. As in all cases pushing was associated with overall body movements, this may indeed be the case. However, to better describe and understand this behavior, quantifications of the flow are needed, for example using PIV. In addition, the hind limbs were also used for prey manipulation in a shredding behavior (Avila and Frye, 1978; Chum et al., 2013), where the claws on the toes of the hind foot are used to tear the prey to pieces. However, this behavior was exclusively observed when

**Table 3. Results of the univariate ANOVAs testing for differences between prey of different mobility and size**

	d.f.	F	P
Prey mobility			
Factor 1	1,54	5.62	0.02
Factor 2	1,54	4.44	0.04
Factor 3	1,54	2.63	0.11
Factor 4	1,54	4.62	0.036
Factor 5	1,54	4.20	0.045
Prey size			
Factor 1	2,54	58.14	<0.001
Factor 2	2,54	3.29	0.045
Factor 3	2,54	0.02	0.99
Factor 4	2,54	2.58	0.09
Factor 5	2,54	1.75	0.18
Interaction			
Factor 1	2,54	13.54	<0.001
Factor 2	2,54	8.43	0.001
Factor 3	2,54	1.44	0.25
Factor 4	2,54	1.08	0.35
Factor 5	2,54	1.1	0.34

Bold entries indicate significant differences between prey of different mobility and size ( $P<0.05$ ).

manipulating large elongate prey that presumably are too long to swallow whole.

Prey size significantly influences the capture behavior adopted by *Xenopus laevis*, with the capture and transport of small prey being largely dependent on the generation of a water flow (suction), whereas larger prey are often manipulated with the hands. Moreover, prehension strategies are also dependent on prey mobility, with differences being especially noticeable for small prey. Interestingly, a strong interaction effect between mobility and size was noted. This implies that the manipulation strategies are dependent on both size and mobility at the same time, but that size differentially impacts the behavior depending on whether prey are mobile. Interestingly, in *X. laevis* mobility induces hand use for small prey. In strepsirrhines it has also been observed that manual grasping increases for mobile prey (Ward and Hopkins, 1993; Reghem et al., 2011; Scheumann et al., 2011; Toussaint et al., 2015). Large prey automatically involve the use of the hands in *X. laevis*, irrespective of mobility, and involve stretching, laceration and wiping behaviors. Interestingly, small mobile prey are further associated with use of the left hand specifically. This is in accordance with the literature on primates, where left hand grips have been demonstrated to be faster (Ward, 1998) and thus potentially more suited for the capture of small mobile prey. In contrast, large prey involve more bimanual grasping, likely because single hand grasps do not allow the animal to maintain a firm grip on the prey. Intermediate sized prey were associated with a preferential use of fingers II–III, which are used in a scissor-like grip to capture and manipulate prey. In arboreal frogs this grip is used for holding on to narrow substrates during locomotion (Herrel et al., 2013), suggesting that this grip may be well adapted for grasping objects of intermediate size. Possibly this is due to the fact that this grip is stronger than grips involving other fingers, but this remains to be tested. The middle two fingers are, however, the longest ones and may as such provide a more secure grip.

To conclude, our study has shown that *X. laevis* has a complex repertoire of prehension and manipulation that is adapted to the properties of prey. Thus, frogs may be an ideal model system to explore the evolution of grasping and complex manipulation given that several taxa have independently evolved manual grasping and manipulation behaviors (Gray et al., 1997). Moreover, some arboreal frogs (*Phyllomedusa* and *Chiromantis*) even have a first finger that is opposable and has a specialized muscle associated with it, allowing them to perform precision grips (Manzano et al., 2008). This condition is also observed in the frog *Pseudis*, a genus of hylid that has returned secondarily to an aquatic habitat (Sustaita et al., 2013). Thus, although grasping in anurans appears to have originated in different ecological contexts, the most complex forms of grasping may be associated with an arboreal lifestyle. Further studies exploring how frogs grasp and manipulate prey may thus be especially insightful in deepening our understanding of the environmental contexts that gave rise to complex grasping and manipulation in vertebrates.

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#### Competing interests

The authors declare no competing or financial interests.

#### Author contributions

Conceptualization: A.H., E.P.; Methodology: A.A., M.A., T.D., A.H., E.P.; Validation: A.H., E.P.; Formal analysis: A.A., A.H., E.P.; Investigation: A.A., M.A., A.H., E.P.; Writing - original draft: A.A., M.A., T.D., A.H., E.P.; Supervision: A.H., E.P.; Funding acquisition: E.P.

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