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On Preyshaking ("Death-shaking") in Lacertidae

Johannes DAUTH

1040 Wien, St. Elisabeth-Platz 6/31, Austria

INTRODUCTION

"Death-shaking" as a behaviour-pattern is mostly known from the Carnivora /Seitz, 1950; Eibl-Eibesfeldt, 1950; Tembrock, 1958; Heimburger, 1961; Leyhausen, 1965/ and carnivorous marsupials /Ewer, 1968/. It is also known from reptiles /Honegger and Heusser, 1969; Hemmer and Schipp, 1970; Luttenberger, 1977/ but it is only mentioned very superficially and in some cases even incorrectly. Weber /1957/ and Honegger and Heusser /1969/ suppose a fixed connection between seizing the prey and shaking; Dobroruka and Horáčková /1973/ describe vertical shaking in the genus Lacerta. Only Luttenberger /1977/ analysed "death-shaking", in Dracaena guianensis, by a slow-motion film. No author defines the different elements of the motion; nothing is known about releasing factors or effects /"functions"/ of "death-shaking", and nowhere is "death-shaking" exactly defined. This paper now will discuss these aspects.

THEORETICAL ASPECTS

The term "death-shaking" includes the function of killing the prey, and is used within different groups of animals as if it were a homologous behaviour-pattern. But the function of killing the prey is very seldom realized, and homology of this behaviour is not evident. By now the neutral term preyshaking /Dauth, 1981/ is used and defined as follows: preyshaking is a continuous side to side swinging of the head within the functional system "feeding-behaviour" /overpowering, comminution, food-consumption/, /see Fig. 1/. Usually thereby the prey is held in the mouth. The head may swing only once up to the axis or several times to and fro across the axis. The horizontal plane of the head may turn up to an angle of 90 degrees. The entire body can be affected by the motion.

ANALYSIS OF THE MOTION

In order to simplify the description of the preyshaking-motion, some terms were introduced by the author /Dauth, 1981 and 1983/: shake, shake-sequence, shake-process, shake-rate "r", swing, frequency, amplitude, shake-violence, shake-endurance and shake-intensity are the most important elements of preyshaking behaviour. The break-down of the preyshaking-motion enables description of a movement pattern. This pattern is as a norm a taxonomic unit and an important basis for homologizing behaviour. This is

also illustrated by the film "Podarcis melisellensis /Lacertidae/ - Beuteschütteln /"Totschüttelbewegung"/", /Dauth, 1981/. However, homology of behaviour is not only based on normalized movement-patterns. Releasing factors, modifying factors, motivations, functions, evolutionary remainders and many other factors are important.

RELEASING AND MODIFYING FACTORS

By means of different series of field and laboratory tests, releasing and modifying factors of preyshaking have been studied. The following releasing and modifying factors could be recognized: 1. Relative size of the prey object. 2. Motion of the prey. 3. Appendages of the prey. 4. Contact stimulus at the snout of the lizard.

Additionally, the following modifying factors could be demonstrated: 5. Ontogenesis /age of the animal tested/. 6. Captivity /duration, laboratory conditions, etc./. 7. "Hunger" /length of fasting/.

Table 1. Podarcis sicula: Positions of comminution of Locusta migratoria

Position Nr.:		1	2	3	4	5	6	7	8	9	10	11	total	ø
l1	n	1		3		2	7	6	5	2			26	6,2
	ø													
r1	n	1		2	1	7	5	5	6	1			28	6,0
	ø													
l2	n			1	3			4	5	3	6		22	7,7
	ø													
r2	n				3	5	1	2	4	6	3		24	7,2
	ø													
l3	n	6	8	8	12	1	3						38	3,1
	ø													
r3	n	15	10	6	3	2	2						38	2,3
	ø													
lI	n	7	7	13	6	1		3					37	3,0
	ø													
rI	n	9	11	3	6	4		2					36	2,7
	ø													
lII	n		1	1	2	5	7	1	1	3	3		24	6,2
	ø													
rII	n		1		1	7	6	3	3	1	3		25	6,4
	ø													
h/t	n										1	11	12	10,9
	ø													

l1/r1: left/right fore-leg, l2/r2: second pair of legs
l3/r3: left/right hind-leg /saltadorial legs/
lI/rI : first pair of wings, lII/rII: second pair of wings
h /r : head/torso
n : number of observed comminution-procedures
ø : mean-positon of comminution
Position Nr 1 - 4: first part of comminution
Position Nr 5 - 10: second part of comminution
Position Nr 11 : third part of comminution

FUNCTIONAL ASPECTS

The functional analyses of the preyshaking-motion have demonstrated that the shake-process is divided into three parts, corresponding to three "functions" /effects/, /see Tab. 1/:

1. Overpowering the prey /organs of locomotion, e.g. saltatorial legs, get separated, orientation gets disturbed or the prey is killed by shaking/.

2. Ripping of limbs of the prey /limbs that are troublesome during food consumption or that are not eaten are ripped off/.

3. Comminution of the prey.

Preyshaking does not only occur immediately after seizing the prey-object. You can see it often during mastication, combined with pauses. Frequently the prey-object gets lost after shaking, especially when a limb is ripped off and the real prey-object escapes. In the first phase of the shake-process the effect is mainly overpowering the prey, while in the second and third part it is the comminution of the prey. Very seldom the prey-object is killed by prey-shaking. Seen in these functional terms, useless "death-shaking" turns out to be effective preyshaking. Considering where we should start to deal with homology in behavioural science, this particular investigation shows that only the pure motion pattern of preyshaking can be homologized, at least for the Reptilia. Out of this, different behaviour patterns with different effects have developed, according to morphological diversity, ecological adjustment and niche-selection.

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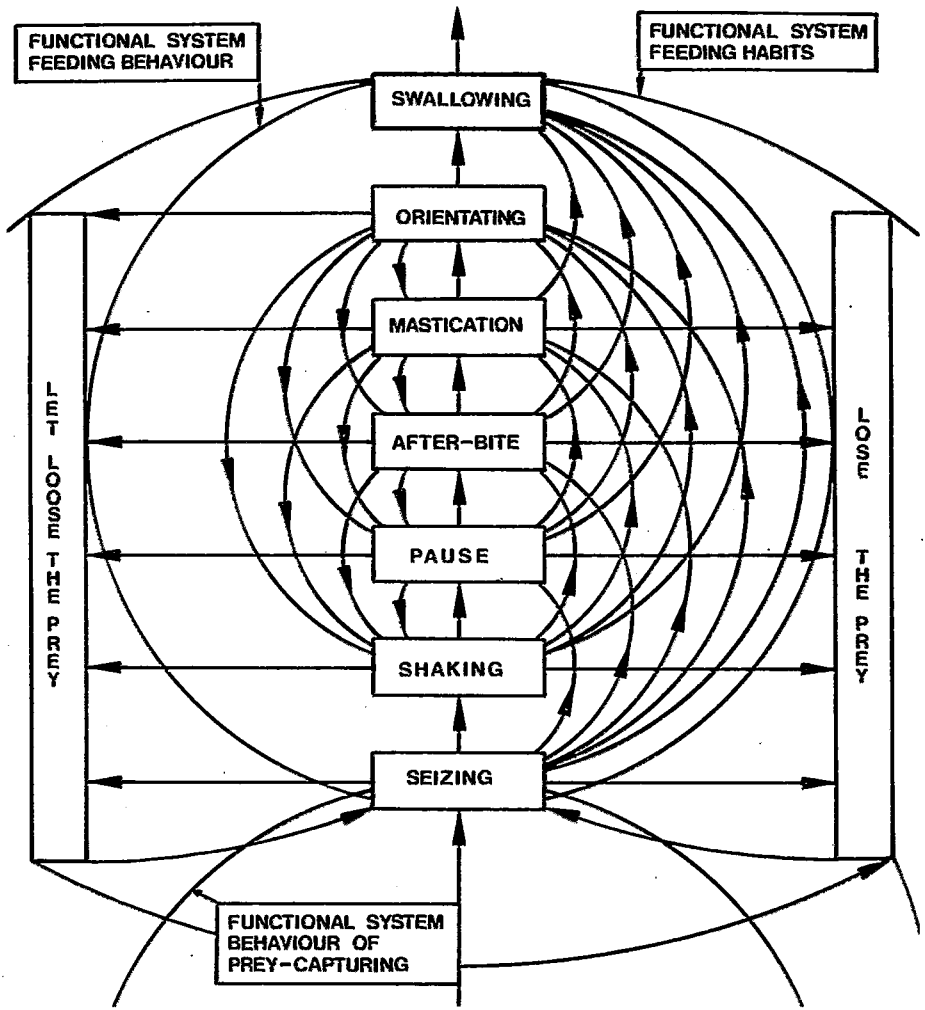

Fig. 1: Possible sequences of feeding behaviour in Lacertidae.