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Role of experience and maturation in barn owl predatory behaviour

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ABSTRACT

The predatory behaviour on mice by sample of seventeen captive barn owls (*Tyto alba*) was studied. The owls were divided into two groups according to their age when they entered the Rehabilitation Centre used for this study (either adults/subadults, i.e., with previous predatory experience in the wild, or as fledglings, without any experience of prey catching). The few differences between the behaviour patterns of the age groups suggested that predatory behaviour is mostly under genetic control. While most adult birds caught the mouse, only four young out of eleven studied did so. Both groups showed a decreasing trend in the latency of predation. The young birds were confused or in conflict when facing the prey, and in some cases the owl approached the mouse closely and then returned to the perch to begin a complete predatory sequence again. Three young birds of those that did not hunt were tested six months later. Two of these three young caught a mouse without any evident difficulty. The behaviour displayed by young birds and some patterns indicate that a maturation process is likely influencing the development of the predatory tendency, and do not fully support the hypothesis of the existence of some temporally well-defined periods.

KEY WORDS: Predatory behaviour - Maturation - Experience - Barn owl - *Tyto alba*.

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INTRODUCTION

The barn owl (*Tyto alba*) is a peculiarly skillful predator. Unlike most other Strigiformes species, it is capable of predation even in the dark (Mikkola, 1983). Its performance is not related to a better sight in low light; other nocturnal raptors, such as the tawny owl (*Strix aluco*) and the long-eared owl (*Asio otus*) are in this respect more proficient (Mikkola, 1983). It relies, instead, on its sharper sound sensitivity and to its ability to integrate visual and auditory signals (Bunn *et al.*, 1982). The barn owl is most sensitive to sound frequencies between 6 and 9 kHz, an adaptation suited for localizing sounds produced by micro-mammals moving in the brushwood (Konishi, 1973).

The peculiar predatory ability of the barn owl seems to develop spontaneously, because the young birds do not try to hunt as long as the parents feed them (Ille, 1991), but once this ends they appear to be as effective as adults (Ille, in press, quoted by Ille, 1991). This ontogenetic process suggests that the predation patterns of this species are subject to a «maturation» process. A similar process is advocated for the stereotyped, species-specific behaviour described for the tawny owl (*Strix aluco*), a closely related species (Meyer-Holzapfel & Räber, 1976). As such, it should be a function of age and independent of experience.

On the other hand, Knudsen *et al.* (1982) and Knudsen & Knudsen (1986, 1990) emphasize the role of experience in the barn owl's development of an even more stereotypic behaviour. In their experiments, birds of different ages were requested to localize a sound and a light source point when their auditory system was severely altered. Their learning ability to localize the source appeared to depend on two well-defined age periods. The first one (the «sensitive» period) ends at the age of 8 weeks; birds exposed to altered conditions during this phase are at first unable to integrate visual and auditory stimuli correctly, but will readily learn to adjust for the wrong cues. The second period (the «critical» period) is much longer, extending to the 29th week of age. Among the birds trained to overcome their abnormal perceptions, only those which can experience normal conditions during this phase will ever be able to react correctly again.

The identification of two age periods involving a modification of the barn owl learning abilities raises the hypothesis that its whole predatory behaviour is also affected by experiences undergone in those periods. In particular, we aimed to study how the predatory behaviour might be affected when the birds do not have any opportunity to prey during the first weeks of their life. One might wonder if they need to experience predation in a critical period to be able to behave efficiently later. Besides, will some of the multiple phases of predation (e.g., prey recognition, attack, ingestion) be affected more than others?

It is also of interest to ascertain whether the predatory behaviour of inexperienced young or inexperienced adults will differ from that of a fully experienced bird. Is it then possible to identify age periods crucial for the development of normal predatory behaviour?

The «sensitive» and «critical» periods of the orientation reaction are used as a first reference frame to test the existence of learning stages and to try to give an answer to these questions. We investigated the above hypotheses with a study on the birds provided by a Rehabilitation Centre. Although tested in captivity, the owls were recovered from the wild at different ages (namely, as fledglings or as adults), which guaranteed they had or had not previous predatory experience.

MATERIALS AND METHODS

The birds used were all wild barn owls. They were temporarily housed in common pens at the Raptor Rehabilitation Centre (RRC) owned in Parma by the Italian Society for the Protection of Birds (LIPU). The birds were recovering from various injuries or found as fledglings outside the nest. The sex of the adults was not known, as no reliable method of sexing was found in the literature (cf. Cramp, 1985).

The birds were housed in a 4.60 × 4.60 m size pen and never offered live prey (cf. Csermely & Agostini, 1993, for details), being fed twice daily with chicken carcasses, as requested by the RRC routine, put on a platform located in the middle of the pen. Owls of both groups were offered no live food until testing. Other details on the pen's layout can be found elsewhere (Csermely & Agostini, 1993).

Each bird was then tested individually with a live prey (C3H strain laboratory mouse, agouti phenotype). There was no previous training on dead mice. Our aim was to ascertain the ability of barn owls to catch a live, natural prey after a prolonged period of feeding on a completely different type of food. In the case of fledglings we could get information on the ability of owls to hunt a potential prey on the first encounter. Besides, there was also the applied aspect to ascertain whether prolonged feeding in captivity with chicken carcasses was detrimental to birds to be released.

The birds were all in perfect physical condition and were chosen only when ready for release. The tests were carried out in the same test pen and with the same procedure as described elsewhere (Csermely *et al.*, 1989, 1991) (Fig. 1). For this study the prey was introduced into the test pen through a black perspex tube projecting over the elevated platform.

The tests were carried out immediately after sunset. The time was adjusted over the study period in order to compensate for daylight variations. The barn owls entered the test pen two days before testing to become used to the new environment. They were offered no food over this period to intensify and equalize their predatory drive (Mueller, 1973; Marti & Hogue, 1979).

Each bird was tested once each day for five consecutive days. The test lasted 60 min or until prey was captured. In the case of successful predation, the owl was allowed to feed on the mouse. Two age groups were first tested:

Adults (AD): which entered the RRC as adult or subadult, with predation experience in the wild.

Fledglings (FL): which entered the RRC as fledgling, without any predatory experience.

Twenty-three owls (12 AD and 11 FL) were used in this study. The FL birds were tested when about 80 days old. A sample of three of them was tested again six months later in order to ascertain their predatory ability. Thus, they can be considered as a sort of third experimental group:

Inexperienced Adults (IA): which entered the RRC as fledgling and were tested when (sub)adult but without having any experience of predation.

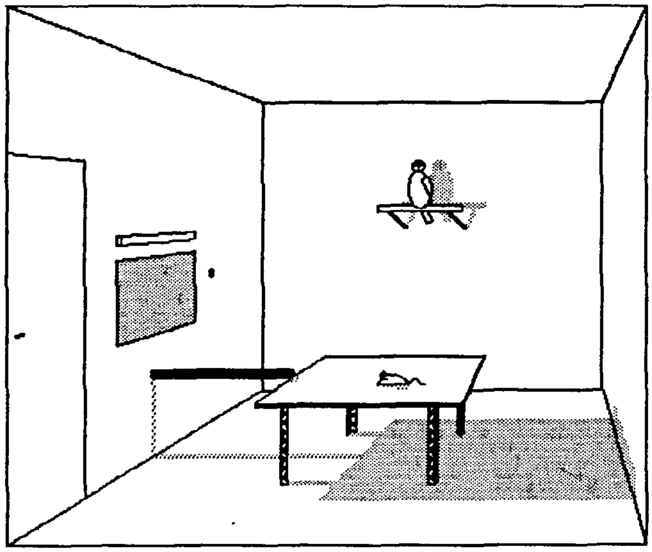

Fig. 1 - A perspective view of the test pen. On the left side the one-way window used for direct observation.

The data were analysed with the Binomial test (Siegel & Castellan, 1988) to evaluate frequencies, the Mann-Whitney U test for comparing data between groups, and Pearson's r correlation coefficient with exponential regression model [$y = e^{(a+bx)}$] for the data trend during the tests.

RESULTS

A total of 61 successful prey captures were recorded (Table I), performed by 10 AD birds and 4 FL birds. One AD owl suddenly died before the last test, although behaving normally during the previous one. The AD owls were successful in 78.0% of tests, while FL birds only in 27.3%.

Activity before predation

The birds very rarely moved after the prey entered the test pen. No flights occurred among the AD owls at all, and only one movement on the perch was recorded,

TABLE I - *The observed frequency of both direct and indirect capture on the mouse in each group of barn owls in each test.*

Group	Type of predation	Test-1	Test-2	Test-3	Test-4	Test-5	Total
FL	Direct	1	2	3	3	4	13
FL	Indirect	0	1	0	1	0	2
AD	Direct	5	9	8	10	9	41
AD	Indirect	2	1	2	0	0	5

during the first test. The flights were considered when the owl started from the perch, flew along the pen, even over the platform, and landed on the perch again or on other structure of the aviary. The attack flight performed to catch the mouse was then not recorded as a «flight». In contrast, FL birds displayed exactly 200 flights, particularly during the fourth test (n = 115). These owls performed 10 movements on the perch.

Preening was the most frequent activity observed, particularly among FL birds. The mean frequency of preening was very high during the first two tests, but much lower in the last ones among both AD and FL owls (Fig. 2). However, FL owls displayed more preening than AD birds only in the third test ($Z = 2.189$, $n = 23$, $P < 0.05$). Before the prey attack, other types of movement, like leg stretching or «yawning», were sometimes recorded. These were likely connected to a transitory lack of interest in the prey. During this phase of the test and regardless of age the barn owls showed alternating periods of greater and lesser attention to the prey. They invariably appeared very concerned with the prey activity immediately after its appearance and for the first 10-12 min. If not attacking over this period, they showed some intermittent shorter periods of high attention along the test.

Predatory behaviour

Three of the 10 hunting AD owls caught the mouse only from the second test onwards, while the other

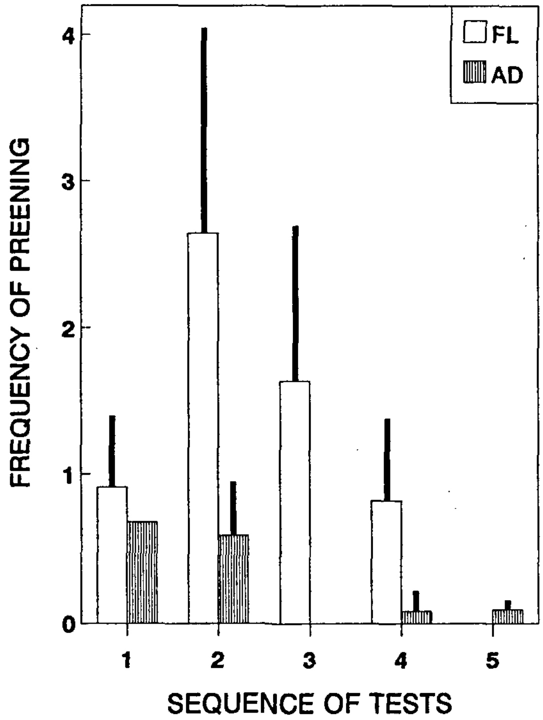

Fig. 2 - The observed mean (± SE) frequency of preening per bird in each group in every test.

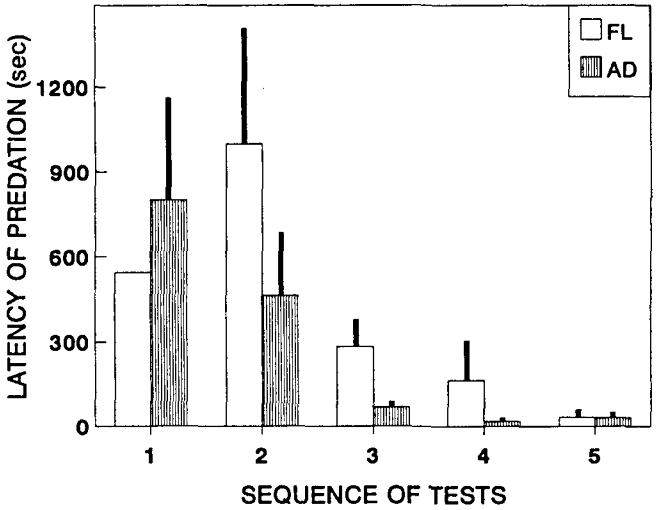

Fig. 3 - The mean (+ SE) latency of predation per bird in each group in every test.

seven hunted during every test (Table I). One of the 4 hunting FL birds caught the prey regularly, two others from the second test onwards, and the fourth bird only from the fourth test. Both groups showed a strong tendency to reduce the latency of predation during the tests ($r = -0.566$, $df = 44$, $P < 0.001$ for AD; $r = -0.720$, $df = 13$, $P < 0.01$ for FL) (Fig. 3). Differences between the two groups were significant only in the third test ($Z = 2.113$, $n = 13$, $P < 0.05$).

Most often, both groups of birds landed directly on the prey (Table I). Indirect predation involved generally the following sequence: the owl landed on the platform immediately pursuing the prey until grasping it on the platform, or on the ground if it had jumped off when the bird landed. In one case, an AD bird was not able to catch the prey immediately after landing. Instead of persisting, the owl returned onto the perch starting the whole sequence anew. A similar behaviour was recorded in one FL and two other AD owls that attacked in the direct way. After the owl landed on the mouse's back and contacted it with the toes, the prey escaped, remaining either on or off the platform. The owl stopped the predatory sequence, returned to the perch and immediately tried it again, but paying more attention to the prey's movements.

While the behaviour patterns before predation were rather variable between the owls, those displayed after the capture were relatively homogeneous. The prey was generally captured with only one foot (Table II); the left one was used only rarely by AD birds ($P < 0.01$, Binomial test) and only once by FL owls ($P < 0.025$, Binomial test).

Once hold, the prey was killed in a very stereotypical way, regardless of the group. The barn owl stood on the mouse and used its bill to grasp the neck, quickly pulling right and left. Such an action was likely to cause breaking or dislocation of the cervical vertebrae. At the same time, the foot grasp induced a strong pressure on the mouse's chest, probably preventing breathing. We recorded this

TABLE II - *The observed frequency and the relative percentage of ascertained prey capture with either foot or both feet in each group of barn owes.*

Group	Foot used for prey capture			Total
	Left	Right	Both	
FL	1 (7.7%)	8 (61.5%)	4 (30.8%)	13 (100.0%)
AD	7 (16.7%)	21 (50.0%)	14 (33.3%)	42 (100.0%)

procedure in 56 out of the 61 total occasions. In the remaining four kills the owl simply stood motionless on the prey, which presumably died by suffocation. In another case the owl grasped the mouse from the anterior quarter and pecked it viciously on the back and abdomen.

The latency before ingestion, i.e., the time elapsing from prey capture to the start of its ingestion, is likely a measure of the time necessary to induce death of the prey. Although progressively reduced, it did not vary significantly over the tests among the AD owls (Fig. 4). FL birds, instead, showed greater decrease in this latency time over the tests ($r = -0.657$, $df = 12$, $P < 0.02$).

Behaviour of IA owls

Three FL owls that did not attack the mouse were tested again six months later, i.e. at an age of about 37 weeks, well beyond the end of the alleged «critical period». During this interval they were never offered any live prey. One of them did not hunt at all again. A second

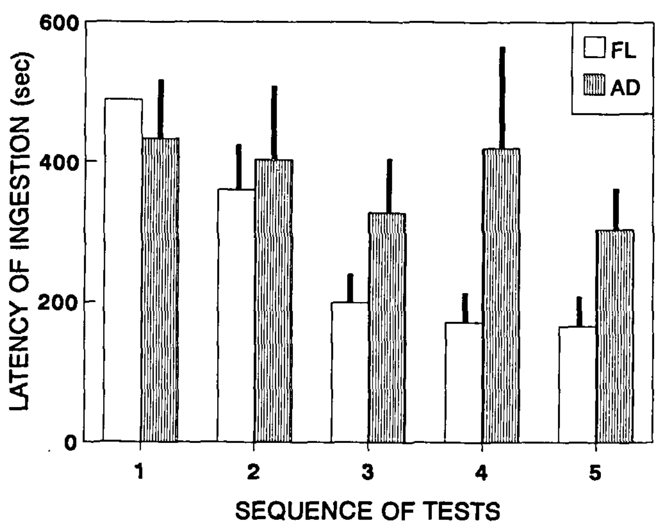

Fig. 4 - The mean (+ SE) latency of ingestion per bird in each group in every test.

one displayed a typical conflict behaviour (flights and movements on the perch) on the first test, but carefully attacked the mouse indirectly after 220 seconds grasping the tail with its bill. As the mouse struggled the owl left it and returned to the perch, falling asleep a few seconds later. The next day (second test) it tried to capture the mouse in the same way, but the prey was able to escape between the toes and jumped off the platform, where it was finally killed 74 seconds after the start. The same owl, after a latency period of 22 seconds, landed directly on the prey in the third test grasping it a few seconds later on the ground under the platform.

The third owl, that had performed several conflict behaviours during the original tests, did capture the mouse on the third test, after a latency of 93 seconds and without any previous activity. The latency became progressively shorter during the remaining tests, reaching a minimum of only one second in the fifth test.

DISCUSSION

This study reveals many and very great similarities between the predatory behaviour of adult and young barn owls, even when facing live prey for the first time (Ille, 1991). The birds did not seem to have difficulty in catching the mouse. Adults had experience of these prey in the wild but were prevented for long time in captivity. On the other hand, fledglings showed more difficulty but this was likely due to their conflict towards the prey, not to their inability to recognize the mouse as a prey. In fact, two owls were ready to hunt the mouse on the first test.

The killing technique between groups is very similar too, viz. likely inducing suffocation, similarly to what is suggested in other raptor species such as the kestrel (*Falco tinnunculus*) and the buzzard (*Buteo buteo*) (Csermely *et al.*, 1989, 1991; Csermely, 1993). Moreover, the barn owls certainly become progressively used in some way to the environmental conditions during the tests, as shown by the continuous reduction of predation latency and disappearance of the conflict patterns that were recorded mainly in the early tests. Some birds did refuse to hunt in the early tests, but never after a successful capture. On the other hand, the lesser values observed for the latency of ingestion confirm that while the search phase, i.e., the behaviour sequence prior to capture, is potentially highly variable, this is not so for the consummatory phase, which is instead more stereotyped (Curio, 1976).

A certain degree of encephalic lateralization seems to emerge from the preference for using the right foot for prey grasping (Rogers & Workman, 1993). Such lateralization could be influenced later with predatory experience (Ille, 1991) as indicated by the proportion of AD owls that used the left foot, or both, for prey capture.

The decreasing trend for the latency of ingestion in FL owls, moreover with constantly lower values than those of AD birds, could be due to a strong need of food, typical of this phase of the ontogeny, and maybe to a selected, and nowadays innate, eagerness to prevail the begging siblings (Baudvin, 1978, quoted by Mikkola, 1983; Ille, 1991). Five of the FL owls tested were not true siblings but, being kept together at the RRC, and being almost contemporaries, they can be considered as siblings. This hypothesis is supported by the two oldest FL owls: they were those capturing the mouse immediately in the first test. The conflict patterns displayed by the other three younger FL birds could be the result of their social submission during the nestling period.

A conclusion emerging from this study is that young barn owls are able to catch a prey even after the sensitive period, although their predatory behaviour is, on the whole, more hesitant than that of adults. In contrast to Ille's hypothesis (Ille, in press, quoted by Ille, 1991), it is possible that experience plays an important role in the development of such behaviour, but we must point out that our FL birds truly experienced the prey for the first time in their life. Moreover, owls without experience are still able to hunt after the end of the critical period, as shown by our IA birds. In fact, they are as skillful as contemporaries with experience. We thus suggest that predatory behaviour is not affected by whether the period is sensitive or critical. The lack of importance of the two periods and the more frequent indirect predation can be explained almost fully by Meyer-Holzapfel & Räber's (1976) theory. They stated that the predatory behaviour of the tawny owl is based on a maturation process that governs its development when about four to six weeks old. There are no sensitive or critical periods and the young bird goes through a conflict period, due to the contemporary experience of the predatory drive and fear of the prey. What we recorded among the FL barn owls fits this description very well. Moreover, while the patterns of barn owl predatory sequence are confirmed to be likely very stereotyped and probably genetically controlled (Ille, 1991), as in the tawny owl (Meyer-Holzapfel & Räber, 1976), the same is not true for prey recognition, which seems due to learning of prey characteristics at first meeting and at any age.

Finally, the cases when the owl, both adult and young, stopped pursuing the prey and, after returning to the perch, started a new predatory attempt, are puzzling at first glance. Nevertheless, they may be explained by the cue of toes that are closed around the prey. In fact, in all cases the owl apparently checked its toes, as looking for the prey, before returning to the perch. We suggest that toe closing is possibly a releasing mechanism that informs the owl about successful predation. That tactile information is necessary because of the very high speed of the entire sequence. Contrasting information, i.e., the toes closing but no prey hold, blocks the sequence, which is bound to start again from the beginning.

The owls performed the second attempt apparently less automatically, and this shows the high degree of behaviour plasticity this species has. In fact, it is profitable to use a stereotyped, automatic predatory sequence in order to minimize time, and thus energy, for capture. But if this sequence fails for whatever reason, the owl can easily modify its behaviour, adapting its actions to those of the prey itself, being almost certain to capture it and then acquiring the metabolic energy that can compensate the excess consumed by the necessity of repeating the attempt.

REFERENCES

Baudvin H., 1978 - Le cannibalisme chez l'Effraie *Tyto alba*. Nos Oiseaux, *34*: 223-231.

Bunn D. S., Warburton A. B., Wilson R. D. S., 1982 - The Barn owl. T&AD Poyser, Calton, 264 pp.

Cramp S., 1985 - Handbook of the birds of Europe the Middle East and North Africa. The birds of the Western Palearctic. (Vol. IV, Terns to Woodpeckers). Oxford University Press, Oxford, 450 pp.

Csermely D., 1993 - Duration of rehabilitation period and familiarity with the prey affect the predatory behaviour of captive wild kestrels, *Falco tinnunculus*. Boll. Zool., *60*: 211-214.

Csermely D., Agostini N. A., 1993 - A note on the social behaviour of rehabilitating wild barn owls (*Tyto alba*). Ornis Hungarica, *3*: 13-22.

Csermely D., Mainardi D., Agostini N. A., 1989 - The predatory behaviour of captive wild kestrels, *Falco tinnunculus*. Boll. Zool., *56*: 317-320.

Csermely D., Mainardi D., Agostini N. A., 1991 - Predatory behaviour in captive wild Buzzards (*Buteo buteo*). Birds of Prey Bull., *4*: 133-142.

Curio E., 1976 - The ethology of predation. Springer-Verlag, Berlin, Heidelberg, New York, 250 pp.

Ille R., 1991 - Influence of social behaviour on prey-catching in Barn Owls. Bird Behav., *9*: 7-13.

Ille R. - Prey choice in barn owls *Tyto alba guttata*: Influence of age and experience. (In press, cit. in Ille, 1991).

Knudsen E. I., 1988 - Sensitive and critical periods in the development of sound localization. *In*: S. S. Easter, K. F. Barald & B. M.Carlson (eds), From message to mind: directions in developmental neurobiology. Sinauer Assoc., Inc, Sunderland, 368 pp.

Knudsen E. I., Knudsen P. F., 1986 - The sensitive period for auditory localization in Barn Owl is limited by age, not by experience. J. Neurosci., *6*: 1918-1924.

Knudsen E. I., Knudsen P. F., 1990 - Sensitive and critical periods for visual calibration of sound localization by Barn Owls. J. Neurosci., *10*: 222-232.

Knudsen E. I., Knudsen P. F., Esterly S. D., 1982 - Early auditory experience modifies sound localization in Barn Owls. Nature (London), *295*: 238-240.

Konishi M., 1973 - Locatable and nonlocatable acoustic signals for Barn Owl. Am. Nat., *107*: 775-785.

Marti C. D., Hogue J. G., 1979 - Selection of prey size in Screech Owls. Auk, *96*: 319-327.

Meyer-Holzapfel M., Räber H., 1976 - Zur Ontogenese des Beutefangs beim Waldkauz (*Strix a. aluco* L.). Beobachtungen und Experimente. Behaviour, *57*: 1-50.

Mikkola H., 1983 - Owls of Europe. T&AD Poyser, Calton, 397 pp.

Mueller H. C., 1973 - The relationship of hunger to predatory behaviour in hawks (*Falco sparverius* and *Buteo platypterus*). Anim. Behav., *21*: 513-520.

Rogers L. J., Workman L., 1993 - Footedness in birds. Anim. Behav., *45*: 409-411.

Siegel S., Castellan N. J. jr., 1988 - Nonparametric statistics for the behavioral sciences. McGraw-Hill, Inc, New York, 477 pp.