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Adaptive details in the comparison of predatory behaviour of four owl species

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ABSTRACT

The predatory behaviour of four owl species, tawny owl (*Strix aluco*), long-eared owl (*Asio otus*), little owl (*Athene noctua*) and barn owl (*Tyto alba*), was compared. The birds were wild individuals temporarily in captivity for rehabilitation and were tested before release into an outdoor pen. Between four and ten birds per species were individually tested by offering a laboratory mouse used as prey. The resulting sequence of the predatory behaviour patterns was homogeneous among the species. The latency to attack was similar and there was a tendency to prefer direct attacks, i.e. landing onto the prey directly, instead of indirect ones, i.e. landing a few centimetres from the mouse. However, tawny owls used the former attack only. The various degrees of specialisation to hunt small mammals is reflected by the grip location: the barn owls strongly preferred to seize the mouse on the head, while the little owls preferred the trunk and the other species preferred either location. Similarly, after grasping the mouse tawny and long-eared owls struck it with the beak, while the little owls performed strikes similar to bites. In contrast, barn owls performed a peculiar torsion of the neck region, instead of a beak strike. We interpret this pattern difference within a basically homogeneous behaviour sequence as evolutionary radiation due to species-specific specialisation of feeding and hunting behaviour.

KEY WORDS: Adaptation - *Asio otus* - *Athene noctua* - Feeding - Owls - Predatory behaviour - *Strix aluco* - *Tyto alba*.

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INTRODUCTION

Hunting behaviour of owls has mainly been studied from an ecological point of view (e.g., Ille, 1992; Sonerud, 1992; Redpath, 1995; Hakkarainen & Korpimäki, 1996) or concerning its impact on prey species (e.g., Koivunen *et al.*, 1996; Bellocq, 1998). However, the ethological analysis is still neglected, although the behaviour patterns displayed by the species are an important indication of adaptation to a specific context and can then be used even to clarify some evolutionary relationships.

Although rather uniform in shape, size, ecological niche and diet, consisting mainly of vertebrates, particularly small mammals, European Strigiformes show some variations in adaptation. Their activity spans from almost strict nocturnal activity, e.g. the barn owl (*Tyto alba*), to mainly diurnal activity, e.g. the little owl (*Athene noctua*) or the scops owl (*Otus scops*) (Mikkola, 1983; Cramp, 1985). Moreover, their food range can be variable, although not greatly, as well, relying almost exclusively on small mammals, as the barn owl or the tawny owl (*Strix aluco*), or largely on insectivorous diet, as the little owl (Bunn *et al.*, 1982; Mikkola, 1983). Therefore, some variations of the predatory behaviour sequence are expected, although the outline of the sequence as a whole is expected to be rather similar between species. In fact, the common phylogeny and similarity in ecological niche are likely responsible for the basic, 'standard' behaviour sequence, although the species belong to two separate families (Tytonidae and Strigidae), but specific adaptations lead likely to limited modifications, whose comprehension can also give some insight on evolutionary specialisation.

This study aimed then (1) to compare the predatory behaviour technique of some owl species in a standardised context, using wild captive birds hunting on a terrestrial prey, such as a small mammal, and (2) to analyse for possible differences ascertaining whether they could be related to specific trophic adaptation and/or phylogenetic divergence.

MATERIALS AND METHODS

We report the outcomes of predatory tests from tawny owls (*Strix aluco* Linné, 1758) (n = 4), long-eared owls (*Asio otus* Linné, 1758) (n = 6) and little owls (*Athene noctua* Scopoli, 1769) (n = 8). Additionally, similar data from adult/subadult barn owls (*Tyto alba* Scopoli, 1769) (n = 10), published elsewhere (Csermely & Sponza, 1995), are incorporated herewith as reference and comparison, since the tests had been carried out at the same location and with the same procedure used for the other species. However, it is necessary to point out that the barn owls described in Csermely & Sponza (1995) made a sequence of five repeated predation tests, while here we consider the first of such predations only.

All individuals were wild adult/subadult birds temporarily kept in captivity for rehabilitation from various injuries at the Raptor Rehabilitation Centre (RRC) managed in Parma by the Italian Society for the Protection of Birds (LIPU). Once physically rehabilitated the birds were housed in a large pen before the release, where they were fed only with dead day-old chicks (*Gallus gallus*). All the individuals tested were chosen among those ready to be released. They had no physical or sensory deficits and their predatory behaviour was then not affected. They were weighed using a digital hand balance to the nearest 5 g. The amount of body fat was estimated by squeezing gently the pectoral muscles. The owls were tested individually in an outdoor experimental pen, 10 × 3.5 × 2.5 m in size, located in a small wood surrounding the RRC. The pen was equipped with a 1.80 m high perch, placed near the back short side of the pen, and with a 60 cm square plastic table (60 cm high), located along the midline of the pen about 1.5 m from the front side. The distance between perch and platform was then about 8.0 m. The rear third of the pen was covered by a roof. The natural light provided a natural photoperiod, but the presence of three 24 W red bulb lights allowed to record the behaviour patterns in dim light.

About three days before entering the experimental pen the birds were treated pharmacologically to remove both ecto-, with PBK, and endoparasites, with ivermectin. The owls remained in that pen for 48 h before testing and were fed once daily with three dead day-old chicks. The tests were performed at dusk, on rain-free days. The owl behaviour was recorded from a blind equipped with a one-way window adjacent to the pen rear short side, next to the table. A slanting pipe starting from the blind allowed one live laboratory mouse (*Mus musculus domesticus*, C3H strain, with agouti pelage) to arrive upon the table at the beginning of the test. These mice were a surplus from the colony of the breeding unit of the Dipartimento di Biologia Evolutiva e Funzionale, Università di Parma. If predation did not occur within 60 min, the mouse was removed from the table and returned to its original cage. The same bird was then tested again on the following day. The latency and duration of the behaviour patterns considered were recorded using four digital stopwatches.

Just before prey ingestion, the mouse was retrieved removing it from the owl's feet. The mouse was then replaced with one dead chick. The mouse was necropsied within 60–90 min to assess the possible cause of death. During the necropsy the mouse was inspected macroscopically but no histological examination was made (cf. Csermely *et al.*, 1998). Unfortunately, it was possible to conduct the necropsy only on the mice captured by tawny and long-eared owls, but not by barn and little owls.

The latency and duration of behaviour patterns were analysed using the Kruskal-Wallis one-way ANOVA (Siegel & Castellan, 1988) as calculated by the SPSS software (SPSS Inc., 2000), while the observed frequencies were compared against the relative expected ones (50% of chance) using the chi-square component '*z*' index (Bishop *et al.*, 1975). The means are given with SE and the probability, set at $\alpha = 0.05$, is two-tailed throughout.

RESULTS

All four tawny owls preyed on the mouse during the first test, while the six long-eared owls equally split the capture of the mouse during the first and the second test. Most barn owls and little owls ($n = 7$ each) preyed on the mouse during the first test, while three barn owls and one little owl captured the mouse during the second one.

Tawny owl

In the early period following prey appearance, the four owls were almost motionless. Although each bird preened (total duration: 67.0 ± 27.3 s), none moved on the perch and two birds only made two flights each within the pen (Table I). The mean latency to fly and to preen did not differ statistically (11.22 ± 0.20 and 4.95 ± 1.18 min, respectively). When catching the mouse, the Tawny owls performed only direct attacks, i.e. the bird landed directly onto the mouse. The mean latency to attack was 20.23 ± 5.31 min. Three owls grasped the mouse at the trunk and only one at the head or the fore part of the body, using always both feet together. Once seized, two owls struck the mouse (frequency: 2.5 ± 0.5 each) with the beak, always to the head as target.

Long-eared owl

Three birds out of six performed some (1.33 ± 0.33 each) movements on the perch, two birds made a few (2.00 ± 1.00 each) flights and four owls preened (total duration 53.0 ± 30.8 s). The mean latency to move and preen were not statistically shorter than to fly (10.80 ± 4.43, 3.74 ± 1.37 and 17.64 ± 10.44 min, respectively), while the latency to attack was recorded 21.00 ± 6.05 min after prey appearance (Table I). The owls performed both kinds of attack considered: direct and indirect, i.e. landing on the table and then grasping the mouse after a few steps. Four owls performed the direct attack and two performed the indirect attack. The former owls attacked earlier than the latter (19.44 ± 6.95 min vs 24.11 ± 15.66 min, respectively), being the difference not significant. The mouse was most often grasped at the trunk ($n = 5$) and only once at the head or the fore part of the body. There was no relationship between type of attack and grip location. These owls used without preference both feet ($n = 3$) or one foot

TABLE I - *The frequency of several behaviour patterns considered before the attack, together with the latency to attack (in minutes) and the frequency of beak strikes to the prey in each species.*

Species	*n*	Freq. of movements	Freq. of flights	Freq. of preening	Latency to attack	Freq. of beak strikes
Strix aluco	4	0.00 ± 0.00	1.00 ± 0.23	3.25 ± 0.75	20.23 ± 5.31	1.25 ± 0.75
Asio otus	6	0.66 ± 0.33	0.66 ± 0.49	2.50 ± 1.12	21.00 ± 6.05	1.67 ± 0.56
Athene noctua	8	4.25 ± 2.22	6.25 ± 3.19	0.25 ± 0.25	13.50 ± 4.26	0.88 ± 0.13
Tyto alba	10	0.10 ± 0.10	0.00 ± 0.00	0.50 ± 0.40	15.23 ± 4.47	1.00 ± 0.00

only (n = 2), the right, to grasp the mouse. The birds gripping the mouse with both feet performed also the direct attack, while those grasping the mouse with the right foot only performed the indirect attack. Four owls, after seizing the mouse, struck it (frequency: 2.5 ± 0.3 each) with the beak, the head being invariably the target of such strikes.

Little owl

After prey appearance, three birds out of the eight used performed both a few (11.33 ± 2.40 each) movements on the perch and some flights (16.67 ± 5.03 each), while only one of these birds preened (total duration: 35.0 s) (Table I). The mean latency to move, fly and preen did not differ: 7.54 ± 1.13, 5.25 ± 0.28 and 7.78 ± 0.00 min, respectively. The mean latency to attack was 13.50 ± 4.26 min; five owls performed the direct attack and three performed the indirect attack. However, although the former owls attacked earlier than the latter (9.16 ± 2.94 min vs 20.72 ± 9.94 min, respectively), the difference was not significant. The mouse was most often grasped at the trunk and rarely at the rear part of the body (five vs two times, respectively). There was no relationship between type of attack and grasp location. The little owls used preferably the right foot (n = 5) to grip the mouse, but sometimes used also the left one (n = 1) or both feet (n = 2). After capture, all the owls but one struck the mouse (frequency: 1.0 ± 0.0 each) with the beak, using a pattern more similar to a bite than to a real strike. The neck and/or occipital region was the invariable target of such strikes.

Barn owl

The ten barn owls did not perform many activities prior to attacking the prey. In fact, only one performed a single movement on the perch (latency: 16.67 min), none flew within the pen and only two birds, different from the one which flew, preened (total duration: 50.5 ± 46.5 s; latency: 7.84 ± 1.68 min) (Table I). The mean latency to attack was 15.23 ± 4.47 min. The owls performed both kinds of attack, without preference for either: seven times the direct attack and three times the indirect one. The latency to attack did not vary with type of attack. The mouse was gripped at any part of the body: at the head or the fore part of the body (n = 3), at the trunk (n = 3) and at the rear part (n = 2). There was no relationship between type of attack and grasp location. The owls often used both feet (n = 3) or only the left foot (n = 4) to grip the mouse, while a single bird used the right foot; it was impossible to ascertain the foot use for two birds. The foot use was not correlated with the type of attack. Once seized, the owls struck the mouse neck region in a specific way: they grasped the neck with their beak, quickly pulling right and left, likely causing the breakage or dislocation of cervical vertebrae. At the same time, the foot strongly squeezed the mouse's chest.

Species Comparison

The comparison of the behaviour patterns between the four species considered revealed that the latency to perform the activities preceding the attack, i.e. the latency to move, to fly, to preen, as well as preening duration did not vary between the species. However, the frequency of preening was greatly different (KW = 12.358, n = 3, $P < 0.01$), tawny owls performing the highest frequency of preening and little owls the lowest (Table I). Although the mean latency to attack was greatly variable between the species, ranging from a minimum of 13.50 ± 4.26 min in the little owl to a maximum of 20.99 ± 6.05 min in the long-eared owl, they were not statistically different.

The owls attacked the mouse after similar latency. They did not usually show any preference for attacking the prey directly or indirectly, only the tawny owl attacking indirectly less frequently than expected by chance (z = -1.114, $P < 0.05$). In contrast, the use of either foot for prey grasping was rather different between species. Considering the feet use frequency as a whole, the long-eared owl as well as the barn owl used both the right foot only and both feet together as frequently as expected by chance. However, the former used the left foot less often than expected (z = -1.074, $P < 0.05$) and the latter more often than expected (z = 1.985, $P < 0.05$). In contrast, while the tawny owl preferred to grasp the prey with both feet together (z = 1.414, $P < 0.05$), using the right foot rarely (z = -1.109, $P < 0.05$), the Little owl did the opposite: it used both feet less often than expected (z = -1.00, $P < 0.05$) and the right foot very often (z = 1.618; $P < 0.05$).

The tawny- and the long-eared-owl did not grip the mouse in a preferred body part; by comparison, the little owl rarely grasped the prey at its fore part (z = -1.183, $P < 0.05$), whereas the barn owl did so more frequently than expected (z = 1.107, $P < 0.05$).

Necropsy

The necropsy was carried out on 10 mice: four preyed upon by tawny owls and six preyed upon by long-eared owls. The preliminary external inspection revealed no skull damage of any mouse (Table II). Skin wounds caused by talons were infrequent (two of the six individuals) in the mice captured by long-eared owls, but very frequent (three of the four individuals) among those captured by tawny owls. Such wounds were not superficial, causing lesions to the muscles below and more or less extensive subcutaneous bleeding. In the case of one of these mice, seized by a tawny owl, the talon cut into the lung.

In only two instances, one mouse seized by a long-eared and one by a tawny owl, the thorax inspection revealed the presence of both clotted and unclotted blood. In the abdominal cavity the same carcasses also had hemoperitoneum, with some amount of unclotted blood. The excision of large vessels, such as the aorta and the vena cava to remove the heart or the necessary

TABLE II - *Type of lesions recorded in the mice killed by tawny owls and long-eared owls during the predation tests.*

Necropsy pattern	*Strix aluco*				*Asio otus*					
	1	2	3	4	1	2	3	4	5	6
Talon wounds on skin	X		X	X			X		X	
Talon lesions on muscles	X		X	X			X		X	
Skull lesions										
Clotted blood in abdomen										
Unclotted blood in abdomen	X									X
Clotted blood in thorax	X									X
Unclotted blood in thorax	X									X
Unclotted blood after heart large vessels excised	X	X		X	X	X	X	X	X	X
Pulmonary petechiae	X			X	X	X	X	X	X	X
Pulmonary suffusions	X	X		X	X	X		X	X	X
Pulmonary perforation			X							
Cardiac petechiae					X	X			X	
Cardiac suffusions				X	X					
Coronary dilation		X	X	X		X	X	X		X

cut of ribs to open the chest, caused a certain amount of bleeding. This occurred in all the mice seized by long-eared owls and in three out of four mice captured by tawny owls.

Some carcasses showed evident petechiae and/or suffusions located on the lung surface. A petechia is defined as a small and sharp-edged red spot while a suffusion is defined as a larger spot with faded edges (Webster's New Collegiate Dictionary, 1973; Dorian, 1988, 1989). The lungs of all the six mice killed by the long-eared owls revealed a few, but evident petechiae and those of five of them showed not very large suffusions. On the other hand, some petechiae were found in two of four mice seized by tawny owls and small suffusions in three of those four mice.

The heart showed the same phenomenon, although less frequently. Many sub-epicardial petechiae were evident in half of the mice captured by the long-eared owls and large suffusions were only observed in one of them. In contrast, the mice captured by the tawny owls never showed the petechiae and only one mouse showed some large suffusions. The heart inspection revealed the frequent dilation of the coronary arteries. This occurred in four of six mice killed by long-eared owls and in three of four mice killed by tawny owls. One of these mice, killed by a long-eared owl, was that one mentioned above getting a talon lesion to the lung; besides, it was the only one mouse having no visible petechiae or suffusions on the lung surface.

DISCUSSION

The predatory behaviour displayed by the four species appears specifically to be rather homogeneous. Nevertheless, there are scattered aspects showing evident, significant differences. The behaviour before the attack is very constant, being the movements on the perch, flights and preening performed similarly between the species. The only difference recorded concerns the frequency of preening, which is, though, possibly related to peculiar individual reactions to the prey in the captivity context. However, this cannot lead us to conclude that the behaviour recorded is altered by captivity, as the above patterns, considered as conflict behaviours, were displayed by a limited proportion of birds. An indirect confirmation comes from the limited number of birds not taking prey during the first test. The only exception to this is the long-eared owls, which split equally their successful attempts between the first and the second test.

The sequence of predatory behaviour patterns is also homogeneous. The four species considered attacked after similar latency and showed the same tendency to have a slight, but non significant, preference for direct attacks. The only strong preference concerning this pattern was the tawny owls, which used this type of attack only. Similarly, there was a slight tendency to grip the mouse at the trunk, i.e. at the centre of the target. However, the barn owl captured the prey on the head more often than expected and the little owl less often than expected. This result is explained by considering that the barn owl is specialised to prey upon small mammals (Bunn *et al.*, 1982; Mikkola, 1983) and gripping them on the head may limit their possible and potentially dangerous retaliation bites. This owl is also known to be able to locate the prey spatially with extreme accuracy, even in darkness (Bunn *et al.*, 1982; Mikkola, 1983; Moiseff, 1989) and can then easily perform high precision grasps. On the other hand, the little owl, although equipped with strong feet, other than being also rather diurnal, is the smallest and the most insectivorous species of those considered here, particularly the southern European population (Zerunian *et al.*, 1982). Its avoidance of head gripping is likely due to lack of specialisation and consequent preference for a firm grasp.

The recorded difference between species concerning the type and location of beak strikes reflects clearly different predatory adaptations. In fact, both tawny and long-eared owls are moderately specialised to hunt small mammals, even in environments such as Italy where invertebrates are abundant (Malavasi, 1995; Capizzi, 2000). Consequently, they targeted the strikes to the mouse's head, similar to some Falconiformes species (Csermely *et al.*, 1991, 1998; Csermely, 1994). This causes damage to central nervous system, limiting the movements and, consequently, any escape possibility. On the other hand, the barn owl confirms its specialisation to hunt small mammals (Bunn *et al.*, 1982; Bosè & Guidali, 2001) performing a peculiar torsion of the neck region, instead of a beak strike, as the other owls. Such a behaviour pattern has never been recorded in the other species considered and, as far as we are aware, was never described in any other owl species. The strikes displayed by the little owl, actually more similar to simple bites, although targeted to the neck region as well, are likely an indication of this species' lack of specialisation for preying upon small mammals.

Finally, the differential use of the feet for prey grasping is somewhat puzzling: in fact, each species seems to have developed its own preference for foot usage when seizing the prey. The tawny owl preferred using both feet and 'refused' using the right foot, while the little owl did the opposite: it preferred the use of the right foot, 'refusing' to use both feet. Both other species considered, although using often both feet, differed greatly in the use of the left foot: in fact, the barn owl used that foot significantly more than expected by chance, whereas the long-eared owl did so significantly less than expected. It is then possible that there is some form of lateralization in foot use for prey grasping at population level (cf. Csermely, 2000). However, the small sample size of this study does not allow for a definitive conclusion.

In conclusion, the predatory behaviour sequence performed by the four owl species is as a whole almost homogeneous, an indication of common ancestry. However, its detailed analysis shows some striking differences, concerned with evolutionary radiation due to species-specific specialisation of feeding and hunting behaviour. According to current phylogenetic views (Mikkola, 1983; Cramp, 1985; Sibley and Monroe, 1990), the barn owl is set clearly apart. In addition, our data show the little owl as moderately different, from the predatory behaviour point of view, from the other species considered, an indication very close to Cramp's (1985) views, who splits the Strigidae family into the two subfamilies Buboninae, containing *Athene*, and Striginae, containing both *Strix* and *Asio*.

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