

Footedness Bias in Hunting Birds of Prey

Davide Csermely

ABSTRACT

Birds of prey use their feet to capture prey, particularly when occurring on the ground, and thus they are good candidates for studies on footedness, i.e. the preferential use of limbs. This preference is still poorly known among birds in general.

Several successful attempts at predation by rehabilitated Falconiformes and Strigiformes were analysed. Those birds' predatory ability is routinely tested to evaluate the success of their release to the wild. One laboratory mouse was usually offered, but other species, ranging from grasshopper to one-day-old chick or small rat, were used as well. Kestrels *Falco tinnunculus* and Common Buzzards *Buteo buteo* tended to grip with only one foot, but without side preference. The foot used in the first test was also used subsequently. In contrast, owl species such as the Barn Owl *Tyto alba* and Tawny Owl *Strix aluco* used mainly both feet. Young Barn Owls were more variable than adults in foot use. In contrast, the Little Owl *Athene noctua*, a rather diurnal owl, showed strong preference for using the right foot only.

Birds of prey then show various degrees of footedness, with limited difference between individuals, and such species differences are likely related to environmental constraints.

INTRODUCTION

Brain functions have for a long time been known to be asymmetrical. Such a difference in functions is connected to different morphology. The brain is defined as asymmetrical (or lateralized) when one side of it is structurally different from the other and/or performs different functions. Brain lateralization has been recorded in many species of birds as well as of mammals (Bradshaw & Rogers, 1993); it is questionable, however, whether this can be considered as a homologous or just as a polyphyletic character.

Brain lateralization, moreover, can be considered at *individual level* or at *population level*. In the first instance the population can consist of one half of individuals that are left-handed while the others are right-handed; as a result, the population itself, as a whole, cannot be defined as lateralized, although consisting of lateralized individuals. In the second case, the population is formed by coherently lateralized individuals, most of them left-handed or right-handed. In this situation it is possible that some sort of selective pressure worked for more than one-half of the population, although ontogenetic factors, other than the selection itself, can promote such a lateralization (Denenberg *et al.*, 1978). In contrast, selective pressure did not exist in the first situation.

Structural asymmetry seems to have a very distant origin. Some of the oldest chordate fossils, the Chalcichordates, appear to be rather asymmetrical in their cephalic extremity (Jeffries & Lewis, 1978); lateralization would then be a primitive character for the Vertebrates.

Birds, particularly birds of prey, are good candidates for the study of the preferential use of limbs for feeding (footedness), as they constantly rely on a firm grasp to hold prey when hunting. Our knowledge of this behaviour in birds is still limited. Footedness has been studied in several bird taxa. For instance, several species of African and Australian parrots, Cockatoos and Goldfinches *Carduelis carduelis* show footedness bias for feeding at population level; in contrast, Great Tits *Parus major* show such a preference only at individual level, while Pigeons *Columbia livia* show no lateral bias of foot use at all (Güntürkün *et al.*, 1988; Harris, 1989; Rogers & Workman, 1993). Since birds of prey have not yet been investigated, this study aims to make a preliminary contribution towards filling this gap by studying the preferential use of either foot in individuals of several species when hunting a terrestrial prey.

MATERIAL AND METHODS

The birds used were all wild individuals of both Falconiformes and Strigiformes, temporarily kept in captivity at a Rehabilitation Centre near Parma (Italy), managed by the Italian Society for the Protection of Birds (LIPU). They were recovering from various kinds of injury and were chosen from among those ready for release. Thus, they were in perfect physical, plumage and flight condition. A variable number of individuals of five species was used: Common Buzzard *Buteo buteo* ($n = 17$), Eurasian Kestrel *Falco tinnunculus* ($n = 73$), Barn Owl *Tyto alba* ($n = 32$), Tawny Owl *Strix aluco* ($n = 7$) and Little Owl *Athene noctua* ($n = 8$).

In order to ascertain their ability to hunt prey, a fundamental requirement for their survival after the release, the birds are routinely tested at the Rehabilitation Centre to assess the probability of successful hunting. They have been individually tested in an aviary specifically equipped to record the predatory behaviour sequence. These tests were also useful in studying some details of the behaviour patterns involved, which are otherwise seen with difficulty in the wild.

I analysed the patterns of several successful predatory attempts by the rehabilitated individuals. The birds were usually each offered daily one adult live or dead laboratory Mouse *Mus musculus domesticus* (C3H strain, agouti pelage), but other species, ranging from young laboratory Rat *Rattus norvegicus* (Brown Norway strain, agouti pelage) to one-day-old chick *Gallus gallus*, adult Lizard *Podarcis muralis* / *P. sicula*, Grasshopper *Chorthippus* sp. and Earthworm *Lumbricus* sp., were used as well, depending on the food adaptations of the predator species.

For the purpose of this study, the parameters of the predatory behaviour considered were (1) which foot, if any, was used by the bird to grasp its prey, (2) the type of approach to the prey (i.e. *direct* = landing on the prey's body or *indirect* = landing a few centimetres away and gripping the prey after a few steps) and (3) the latency of predation, i.e. the time elapsed between the prey's appearance and its capture.

The sex and age of the birds, when ascertained without doubt, were considered. The first test the bird experienced was considered separately; in fact, some birds, but not all, were tested repeatedly, in which case subsequent tests were possibly influenced by the first one.

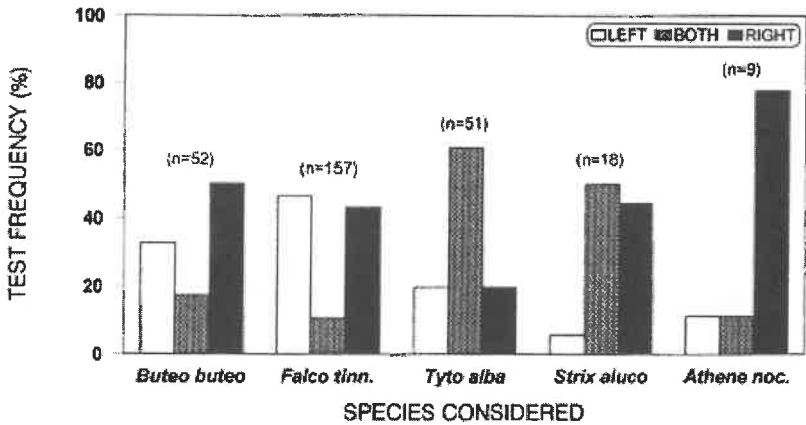
RESULTS

Prey type as well as sex and age of the birds and the latency of predation did not have any substantial influence on foot preference. Figure 1 shows that hawks preferred to use one foot only. However, there was no preference for a particular limb, although a greater proportion of Buzzards used the right one. The foot not involved in prey grasping was used for standing. These species appear then to be lateralized at individual level, as the sample is almost split equally concerning the foot preferred.

In contrast, the Barn Owl and Tawny Owl had tended to use both feet, the Barn Owl in particular. Tawny Owls also used the right foot as well, at a frequency slightly smaller than both feet together.

The Barn Owl, on the other hand, used the left- or right foot with similar frequency. It is then possible that these owl species are not lateralized at all.

Figure 1. The preferential use of feet by the several species used when grasping the prey.



The Little Owl showed completely different results from the other owl species. In fact, it almost invariably used the right foot when gripping the prey, a tendency more similar to that displayed by buzzards and kestrels than by owls. This odd habit can be explained by the rather “diurnal” activity displayed by the Little Owl, that converged towards a “hawk” predatory habit.

Table 1. Number of tests in which either foot was used by age classes with different types of approach.

Species	Age	Approach	Left	Both	Right
<i>Buteo buteo</i>	Adults	Direct	5	4	2
		Indirect	1	0	6 **
	Juveniles	Direct	4	1	10 **
		Indirect	5	2	4
<i>Falco tinnunculus</i>	Adults	Direct	13	11	18 *
		Indirect	20 ***	1	10
	Juveniles	Direct	5	5	7
		Indirect	25 **	0	19 *
<i>Tyto alba</i>	Adults	Direct	5	15 **	3
		Indirect	1	5 **	0
	Juveniles	Direct	1	2	4 *
		Indirect	0	2	1
<i>Strix aluco</i>	Adults	Direct	0	2	2
		Indirect	0	0	0
	Juveniles	Direct	1	4	3
		Indirect	0	3	3
<i>Athene noctua</i>	Adults	Direct	0	1	6
		Indirect	1	0	1

* (More frequent than expected) = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

Both adults and juveniles of any species approached the prey directly and indirectly with similar frequency (Table 1). Adult Buzzards used the right foot more often than expected (Chi-sq. Comp. ‘z’ value = 2.400, $P < 0.01$) in indirect attacks, while the opposite occurred in juveniles (Chi-sq. Comp.

'z' value = 2.236, $P < 0.01$). On the other hand, both adult and juvenile Kestrels tended to prefer using one foot only when performing indirect approach to the prey, but with just a little preference for the left foot (Chi-sq. Comp. 'z' value = 3.007, $P < 0.001$ for adults; Chi-sq. Comp. 'z' value = 2.698, $P < 0.01$ for juveniles), but used one foot or both feet with almost similar frequency when the prey was approached directly.

While Buzzards and Kestrels generally used both feet when approaching the prey directly, the Barn owl constantly used both feet more often than expected during both tests with direct and indirect approach (Chi-sq. Comp. 'z' value = 2.648, $P < 0.01$; Chi-sq. Comp. 'z' value = 2.121, $P < 0.01$, respectively). In contrast, both Tawny Owl and Little Owl used both feet together and the right foot only, respectively, without regard to the type of approach to the prey. Unfortunately, the small sample size prevents any statistical calculation concerning this pattern.

I also ascertained whether there was a constancy in the foot use in repeated tests compared with what was performed during the first test (Table 2). The results show that, once again, Buzzards and

Table 2. Number of birds using the same ($\geq 66.7\%$) or different ($< 66.7\%$) foot than the first test in repeated tests.

Species	1 st Test	Same Foot	Different Foot
<i>Buteo buteo</i>	Left	3	1
	Both	3	0
	Right	10	0
	Total	16 **	1
<i>Falco tinnunculus</i>	Left	22 *	11
	Both	6	5
	Right	22 *	7
	Total	50 **	23
<i>Tyto alba</i>	Left	2	3
	Both	17 **	4
	Right	5	1
	Total	24 **	8
<i>Strix aluco</i>	Left	0	0
	Both	0	2
	Right	5	0
	Total	5	2
<i>Athene noctua</i>	Left	0	1
	Both	2	0
	Right	4	1
	Total	6	2

* (More frequent than expected) = $P < 0.05$; ** = $P < 0.01$.

Kestrels behaved similarly, continuing to use the same foot used in the first test (Chi-sq. Comp. 'z' value = 2.572, $P < 0.01$; Chi-sq. Comp. 'z' value = 2.235, $P < 0.01$, respectively), without regard to which one it was. The same occurred for the Barn Owl too (Chi-sq. Comp. 'z' value = 2.000, $P < 0.01$), but it used principally both feet, instead of only one. Unfortunately, the small sample prevents any statistical analysis in the Tawny Owl and Little Owl.

DISCUSSION

This study shows the existence of a striking bias in footedness between Falconiformes and Strigiformes. Although type of prey as well as sex and age of the bird had no influence on the use of feet, the Falconiformes preferred to use one foot only when grasping the prey. Individuals showed some preference for a particular limb, using the other one for standing. These species appear then strongly lateralized, but only at the individual level; in fact, the tests showed that one leg was used

almost as frequently as the other.

Strigiformes preferred to use both legs to grip the prey. The Little Owl was an exception, as it held the prey mainly with the right foot only. Such an odd pattern can be explained by the rather diurnal activity of the species, leading it to adopt a "hawk-like" predatory habit.

These findings show degrees of footedness at *individual level* in *Falconiformes* and at *population level* in the *Strigiformes*. Such a bias recorded between species seems more related to environmental constraints, principally daylight, than to phylogenetic similarity. In fact, being active with dim light, owls have principally adopted an ambush predation technique and the grip with both feet gives them higher capture probability, enlarging the area useful for contacting the prey's body. In contrast, *Falconiformes* can also account on sight during the last phase of the approach to the prey and this gives them the possibility to use just one foot. Selective factors seem to have affected the species but not individual birds, which are indifferently left- or right-footed.

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Davide Csermely
Dipartimento di Biologia Evolutiva e Funzionale
Università di Parma
Parco Area delle Scienze 11A
43100 Parma
Italy

