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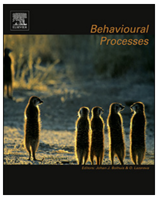

Footedness in Steppe Buzzards (*Buteo vulpinus*)

Reuven Yosef[a,*], Coral Gindi[b], Nufar Sukenik[c,1]

[a] *Ben Gurion University of the Negev – Eilat Campus, P. O. Box 272, Eilat 88106, Israel*
[b] *Rabin High School, 51 Yotam Street, Eilat 88000, Israel*
[c] *Psycholinguistique, Université François-Rabelais de Tours, France*

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ABSTRACT

Asymmetries in handedness/footedness has been demonstrated in many vertebrate and invertebrate species, including humans, but its role and origins are still debated. We studied the ratio of footedness in migratory Steppe Buzzards (*Buteo vulpinus*). We hypothesized that during our raptor banding program we could observe the preferred foot used by the raptor when trying to access the lure in a bal-chatri trap, and that if there was no preference in the population then it would show a 50:50 use of the right or left foot. A total of 367 different Steppe Buzzards were identified and their footedness analyzed. Of these 196 (53.4%) preferentially hit the trap first with the right foot, 148 (40.3%) with the left foot, and 23 (6.3%) appeared to be ambidextrous. In the avian world, predominance is considered to be species specific but mostly right-footed. The migratory Steppe Buzzards also show a predominantly right-sided lateralization. This result could be due to the task/situation that was analyzed; perhaps in a different more tool-like manipulation activity lateralization could be different. We recommend all future researchers that deal in wildlife trapping to also pay attention to this very interesting aspect of wildlife biology.

Introduction

Preferential use of limbs (a.k.a. fore-limb handedness), once thought to be unique to humans, has been studied for many years as a measurable parameter for elucidating cerebral function (e.g. Harris 1983). It is now accepted that the majority of humans, ca. 90%, are believed to be right handed (Holder, 1997; McManus, 2002). However, its role and origins are still debated (Versace and Vallortigara, 2015).

Preferential use of limbs is not exclusive to humans and has been widely documented in a variety of vertebrate and invertebrate species (Ströckens et al., 2013). Versace and Vallortigara (2015) debated concerning whether non-human species exhibit a degree and consistency of functional forelimb asymmetries comparable to human handedness.

As in most cases, research initially focused on humans (e.g., Corballis, 1989), spread to primates (cf. Sugiyama et al., 1993; McGrew and Marchant, 1992), pets and domestic animals (cf. Cats - Wells and Millsopp, 2009; Donkeys - Zucca et al., 2011; Dogs – Wells et al., 2016), and then diversified to other vertebrate and invertebrate zootaxa (see Frasnelli et al., 2012; Jasmin and Devaux, 2015). Generally speaking, in vertebrates the left hemisphere typically controls routine behavior, fine-tuned discrimination, or recognition of conspecifics vocalization while the right hemisphere dominates early detection of unexpected/novel stimuli, behavior in emergency situations, or spatial cognition (cf. Vallortigara, 2000; Manns and Ströckens, 2014).

Functional hemispheric asymmetry is now known to be the fundamental feature of almost all vertebrate brains (cf. Hopkins et al., 2017). Many lateralization characteristics were found to be related to behaviors such as incubation and hatching (Baciadonna et al., 2010), parental care (Karenina et al., 2013), preening and resting (Vidal et al., 2018), and foraging (Hori, 1993; Canning et al., 2011); and to other cognitive and learning processes such as predator avoidance (Lippolis et al., 2002), especially in gregarious species, which may benefit individuals by enhancing the coordination of actions of the school (Bisazza et al., 2000), and associative learning (Letzkus et al., 2006).

Fagot and Vauclair (1991; but also see Prieur et al., 2016, 2017a, 2017b), working with nonhuman primates, found that low-level tasks lead to symmetrical distributions of hand biases for the group, and manual preferences that were not indicative of the specialization of the contralateral hemisphere of the brain. In contrast, they found that behaviors expressed in high-level tasks show asymmetrical distribution of hand biases for the group and seemed to be related to a specialization of the contralateral hemisphere. They concluded that two types of lateralization, handedness and manual specialization, corresponded to the 2 levels of tasks that were distinguished. Studies on tool use in

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[*] Corresponding author.
E-mail addresses: ryosef60@gmail.com (R. Yosef), coralgindi@gmail.com (C. Gindi), nufaryosef@gmail.com (N. Sukenik).
[1] Present address - School of Education, Bar Ilan University, Israel.

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Chimpanzees (hammer and stone use) showed more lateralization than in non-tool use activities (Sugiyama et al., 1993; McGrew and Marchant, 1992).

Of the avian species, most of the earlier studies on laterality were conducted on captive parrots (e.g., Harris, 1989; Ströckens et al., 2013). Snyder and Harris (1997) found that in African Grey Parrots (*Psittacus erithacus*) right-footed individuals had larger lexicons than conspecifics that were left-footed. They found a relation between lateral motor asymmetries in parrots and vocal capacity as indexed by the ability to learn and remember human speech sounds. They concluded that because there is ample evidence for lateralization of the avian brain indicating left hyperstriatal involvement for the long-term consolidation of information for later recall, as well as left hemisphere specialization for the categorization of information. Their results suggested that right footedness in the African Grey parrot represents a behavioral index of contralateral hemispheric specialization for both motor control and for other cognitive functions. However, one must take into account that most of the early studies were evaluated through self-report questionnaires of people who kept pets or in zoos and the reports could be biased, or even wrongly reported, in some cases.

Ströckens et al. (2013) points out that it should be kept in mind that all research on birds is restricted to the hind limbs, and therefore should be careful when comparing them with other tetrapod species. Although they contend that "extensive research on limb preference has been conducted" on birds, their cladogram illustrates the opposite. Only in 11 of the 30 orders have species been studied. Further, only a total of 71 species have been studied of the more than 9000 avian species known to science, with a heavy grouping in the parrots (45%). Of the diurnal raptors only 2 species (Common Buzzard *Buteo buteo*, and Common Kestrel *Falco tinnunculus*) have been studied to date, in captivity, and found a right foot preference for grasping prey (Csermely, 2004).

Hence, in order to understand footedness while hunting at a migratory stop-over site, we studied the hunting behavior of free-living Steppe Buzzards (*B. vulpinus*; see Haring et al., 1999). We assumed that during our raptor trapping and banding program we could observe the preferred foot used by a raptor when accessing the lure, and that if there was no preference in the population then it would show a 50:50 use of either the right or left foot. We hypothesized that, similar to previously mentioned studies of vertebrates, we too would find a preference for right footedness in the migratory population of the buzzards.

1. Methods

This question led us to observe Steppe Buzzards (*B. vulpinus*) in the field during the spring migration seasons of 2016 and 2017. Further, we analyzed all pictures and videos taken between the years 1994–2010 during raptor trapping programs at Eilat, Israel (cf. Yosef and Fornasari, 2000; Yosef et al., 2002, 2003).

Raptor trapping was undertaken with a wide range of traps. However, we included in our analyses only those documented on bal-chatri traps (cf. Bub, 1978; Yosef and Lohrer, 1992) wherein the raptor is forced to access the lure and the use of a specific foot is clear in a series of pictures (N = 177) or on video (N = 159). We did not include in the analyses single pictures and reasoned that they did not necessarily represent the handedness of the bird or the initial attempt. Only the initial foot used was considered to be the preferred limb and all subsequent attempts were not analyzed.

The traps were self-manufactured from hard wire-mesh and the nooses of monofilament (Bub, 1978). We patrolled the date palms in the vicinity of Eilat for perched raptors. Upon sighting a raptor, we drove by slowly and dropped the trap out of the door opposite the perched bird. We kept driving for another 30–40 m and then turned around to face the trap. From within the car we could observe the raptor either stoop at the trap, or land a few meters away and then walk over, or ignore the trap. Using binoculars (Swarovski 10 × 42) we determined the foot initially used by the buzzard to catch the lure. We gave each bird 10 min to approach the trap before moving on in search of another buzzard.

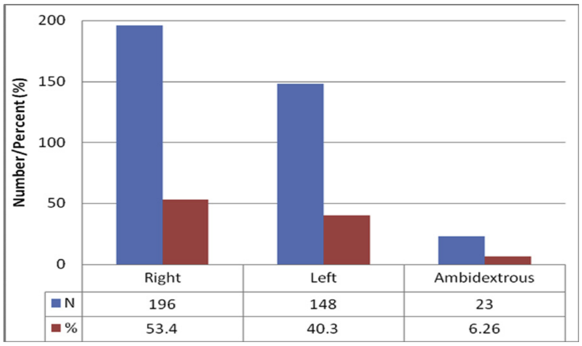

Fig. 1. Handedness in Steppe Buzzard (*Buteo vulpinus*; N = 367) trapped on migration at Eilat, Israel.

During springs 2016 and 2017 we documented 31 Steppe Buzzards that were trapped and banded (Yosef et al., 2019 in Press). In addition, from the archives we analyzed 336 other buzzards photographed on bal-chatris by researchers working in the cooperative raptor trapping and banding program of the International Birding and Research Centre in Eilat, Israel. All of the research was conducted under the research permit of RY, Israeli A bander no. 075.

2. Results and discussion

A total of 367 different Steppe Buzzards were identified and their footedness analyzed when they approached a bal-chatri trap. Of these 196 (53.4%) were observed to preferentially hit the trap first with the right foot, 148 (40.3%) with the left foot, and 23 (6.3%) appeared to be ambidextrous (Fig. 1). The statistical difference between the right- and left-footed buzzards was significant (Chi Square Goodness of Fit Test = 6.70; p = 0.009654). The results suggest that a comparison of the averages gives an impression of right-footedness at the population level for the migratory Steppe buzzard, similar to the findings of Csermely (2004). However, our results agree with Ströckens et al. (2013) who concluded that non-human limb preferences typically show a less-skewed lateralization pattern and there are larger numbers of individuals without a preference in most species compared to humans. Moreover, they think that limb preferences in non-human animals are often less task-invariant than human handedness and are more frequently modulated by external factors and individual characteristics. Our results of 53% right-footedness versus 46% non-right-footedness are far from the 90% versus 10% distribution in humans. In addition, the present study does not allow any conclusions about consistency of individual foot preference or about task-invariance. Both could only be estimated by repeated testing of individual birds, namely in captivity.

These results are of interest because although the Buzzard population appears to be significantly right footed, the relative ratios suggest that ca. 46.6% are either left-footed or ambidextrous. In African Grey Parrots the ratio was similar, 36 right-footed vs 34 left-footed (Snyder and Harris, 1997). In the Caledonian Crows there was no bias for left- or right-footed (N = 2 each; Rutledge and Hunt, 2004). Yet Rogers (1980), (1981), (1989) concluded that both South American and Australian parrots are "predominantly left footed" and that in many of the parrot species the degree of footedness was equivalent to the degree of handedness in human beings. Rogers (1980) tested wild and caged parrots representing nine Australian species and found left foot use in approximately 90% of the trials in eight species and right foot preference in only one species (Fig. 2).

Baciadonna et al. (2010) demonstrated in ostriches (*Struthio camelus*) a population level right-foot preference for all age groups. They also mention that ostriches are known to rely on their right foot to

Fig. 2. Steppe Buzzard (*Buteo vulpinus)* on a bal-chatri trap trying to get to the lure with its right foot.

break the egg shell during hatching, suggesting that precocious laterality at the embryonic and hatching stages might be a precursor of foot preference. Similarly, Vidal et al. (2018) also found a significant predominance of right-footedness in Greater flamingos (*Phoenicopterus roseus*).

It is of interest that brain lateralization is considered adaptive in ecological-field studies because it leads to behavioral biases and specializations that supposedly enhance the fitness of the individuals involved, and it is assumed that strongly lateralized individuals perform better in specific behaviors and are likely to improve their chances of survival. Hence, correctly, Whiteside et al. (2018) questioned what constrains continued exaggerated lateralization to allow for even greater survival probabilities and fitness benefits. In order to answer this question, they measured survival of captive-reared pheasants (*Phasianus colchicus*) and found that individuals with stronger bias in their footedness had shorter life expectancies after release into the wild compared to individuals with weak biases or no footedness. They suggested that although footedness is indicative of more general brain lateralization, different environmental pressures and requirements could explain why continued brain lateralization is constrained even though it may improve performance in specific behaviors. Looking at the bigger picture, there are several examples indicating enhanced performance in lateralized individuals (e.g., Güntürkün et al., 2000; Dharmaretnam and Rogers, 2005; Magat and Brown, 2009; Piddington and Rogers, 2013; Dadda et al., 2015; Bell and Niven, 2016).

Another point that arises is the difference between flocking species and those that do not. Bisazza et al. (2000) investigated 16 species of fish and performed an independent test of shoaling tendency. They found that all gregarious species showed population lateralization, whereas only 40% of the non-gregarious species did so. The results support the Rogers (1989) and Vallortigara and Rogers (2005) hypothesis that population lateralization might have developed in relation to the need to maintain coordination among individuals in behaviors associated with social life. In our case, Steppe Buzzards migrate solitarily, although owing to the large numbers that traverse Eilat, they may appear to be gregarious, and they hunt alone. It is of interest in future studies to see if gregarious migratory raptors, such as Levant Sparrowhawk (*Accipiter brevipes*), show different degrees of lateralization to that of the solitary hunting species.

Hopkins (2006) mentioned that historically, population-level handedness has been considered a hallmark of human evolution, and whether nonhuman primates exhibit population-level handedness remains a topic of considerable debate. He undertook comparative analysis of published data and found that chimpanzees (*Pan troglodytes*) and bonobos (*P. paniscus*) showed population-level right handedness, whereas gorillas (*Gorilla gorilla*) and orangutans (*Pongo pygmaeus*) did not. However, all ape species showed evidence of population-level handedness when considering specific tasks. Meguerditchian et al. (2011) found that baboons (*Papio anubis*) were predominantly right-handed. Overall, the proportion of right-handedness was lower in great apes compared with the ca. 90% right-handedness in humans (McManus, 2002). This is of interest because five (71%; G. Ford, R. Reagan, G. Bush sr., W. J. Clinton, B. Obama) of the last seven presidents of the USA are left-handed.

An exception to the rule appears to be Loggerhead Shrikes (*Lanius ludovicianus*) who were studied handling prey (e.g., Yosef and Grubb, 1993). Yosef (1993) observed that almost always the shrikes handled and transported mice (*Mus musculus*) by using both feet; only when a certain body-mass threshold was exceeded, the prey was transferred to the beak. However, although a great degree of ambidextrous handling of the prey was observed during prey transport, footedness while consuming prey was not. This will require further study as suggested by the pictures included of the handling of grasshoppers, in order to remove the alimentary tract prior to consumption (cf. Yosef and McPherson, 2016).

One must also consider that preferential use of one extremity does not necessarily indicate motor dominance but can also indicate cerebral hemispheric dominance for a special neuronal function. Accordingly, limb use pattern may depend on the nature of the task and the preferred extremity could be inconsistent across different tasks. In vertebrates, the left hemisphere is generally more strongly involved in routine and approach behavior while the right hemisphere dominates detection and response to unexpected and novel stimuli (cf. Vallortigara, 2000; Vallortigara and Rogers, 2005). In this regard, enhanced use of the right foot in buzzards while hitting the trap may indicate a left hemispheric dominance for approaching prey.

We conclude that the subject of lateralization is still being studied intensively but no clear picture appears to be evident. In the avian world predominance is considered to be species specific, but mostly right-handed. The Steppe Buzzards we analyzed show a predominantly right-sided lateralization, but not in an extremely dichotomous manner. This result could be due to the task/situation that was analyzed and perhaps in a different more tool-like manipulation activity lateralization would be apparent. We recommend all future researchers that deal in wildlife trapping to also pay attention to this very interesting aspect of wildlife biology.

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