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MANUAL LATERALITY IN MARSUPIALS

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The monograph provides an overview of current data on the distribution and features of manifestation of lateral functions (asymmetry of use) of extremities in vertebrates and, in particular, in mammals. The monograph focuses on a detailed description of the lateralized functions of the forelimb in quadrupedal and bipedal marsupial mammals studied in captivity and in nature. The emphasis is given to natural manifestations of lateralization in the daily activity of animals. A comparison of lateralization in bipedal and quadrupedal species, as well as a study of lateralization in bimanual manipulations, was previously performed only among primates. The influence of the position of the animal's body on the manifestation of asymmetric use of the forelimb is demonstrated for mammals not belonging to the Primates order. During two expeditions to Australia, the authors obtained data on motor lateralization in the marsupials in nature. This allowed comparing directly the data on the preferences of one limb in animals of the same species in nature and in captivity in identical types of behavior for the first time. The influence of various factors (complexity and nature of the performed action, sex, age) on the direction and force of lateralization in different species of marsupials was assessed. The lateralization of functions of the forelimb is compared in marsupials and placental mammals. The evolutionary aspects of the development of the expressed handedness in bipedal species, including humans, are considered. The book can be of interest to zoologists, physiologists, evolutionary biologists, specialists in the field of brain asymmetry and human evolution, teachers and students of the biological faculties of universities, as well as all those interested in the evolution of man and mammals.

Figures 34, Tables 21, Bibliography 275.

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Introduction

Lateralised limb use by animals is generally defined as an asymmetrical participation of paired limbs in motor tasks [Hook, 2004; Rogers, 2009]. Intensive research in the last decades has demonstrated that some laterality in the use of limbs is a common feature of vertebrates [Ströckens et al., 2013]. It is expressed in the behaviour as the left or the right limb preference for certain tasks [Bianki, 1985; Hook, 2004]. In many vertebrate species, limb preferences were shown to be associated with hemispheric asymmetry [Nudo et al., 1992; Hopkins, Pilcher, 2001; Phillips et al., 2005; Dadda et al., 2006; Hopkins et al., 2007; Rogers, 2009; Hopkins, Nir, 2010; Brown, Magat, 2011a]. Limited available evidence indicate that lateralised forelimb use may be biologically advantageous for an individual [Lorincz, Fabre-Thorpe, 1996; Marchant, McGrew, 1999; Magat, Brown, 2009]. These advantages, such as a higher efficiency of actions [Magat, Brown, 2009; Flindall et al., 2013; Mangalam et al., 2014] and a lesser time expenditure for coordination and initiation of movement [Papademetriou et al., 2005], may explain the wide occurrence of lateralised limb use in vertebrates.

The potential fitness benefits associated with lateralised forelimb use cannot explain, however, the significant variation in the degree of handedness. This variation ranges from species showing neither individual nor population forelimb preferences to species highly lateralised at both individual and population levels (reviewed in Ströckens et al. [2013]). Despite numerous studies of a variety of species, clear theoretical understanding of the factors determining species-typical patterns of lateralisation is lacking. The ‘postural origins’ theory [MacNeilage et al., 1987] remains the most widely discussed explanation for the evolution of handedness within and between different primate taxonomic groups [Hook, 2004; MacNeilage, 2007]. The theory argues that the interspecies variation in manual laterality was shaped by postural adaptations occurring in the course of primate evolution. Recent studies provide evidence in support of the ‘postural origins’ theory (reviewed in MacNeilage [2007], but see e.g., [Lhota et al., 2009] for exceptions), or consider a more general conclusion that feeding ecology and niche structure are the variables shaping the lateralised use of hands in primates [Sfar et al., 2014]. Since the theory has been stated, more than 50 studies on manual lateralisation in non-human primates have been published [Hopkins, 2013], although there is still no consensus regarding the evolution of handedness.

Manual preferences are studied in most detail in placental mammals [Ströckens et al., 2013], with primates being a traditional model group [Hopkins, 2006]. A greater understanding of the evolutionary origin of handedness can be gained by research involving non-primate species. Despite a number of diverse examples [Ströckens et al., 2013], no comparative systematic investigation of manual lateralisation has been conducted in any mammalian group besides the primates. Several common laboratory species, such as mice [e.g., Waters, Denenberg, 1994], rats [e.g., Güven et al., 2003]), domestic cats [e.g., Konerding et al., 2012]), and dogs [e.g., Wells, 2003] have been extensively studied in terms of forelimb preferences. Nevertheless the majority of studies on these species have examined forelimb use in specific experimental conditions, which may influence the natural manifestation of lateralized behaviour [Hopkins, 2006;

Lhota et al., 2009; Rogers, 2010; Schnoell et al., 2014]. Investigations using the observational approach applied in primate studies, but focused on forelimb preferences in non-primate mammals, are extremely rare but needed for further reconstruction of the evolution of handedness.

This study was designed to deeply investigate manual lateralisation in marsupial mammals (Mammalia: Marsupialia). Marsupials, while being almost unstudied in this respect, represent an excellent group to compare to primates in terms of manual lateralisation, not only because they are phylogenetically distant from primates, but also because they display a number of primate-like features. Manipulative dexterity of forelimbs [Iwaniuk et al., 2000] offers opportunities for examining forelimb preferences across various behaviours and for assessing the effect of the manual task characteristics. Furthermore, in primates, manual preferences are known to depend on the posture from which the animal performs the task: bipedal (standing on hind limbs) or quadrupedal (standing on hind limbs and forelimbs) [e.g., Hopkins, 1993; Ward et al., 1993; Westergaard et al., 1997; Blois-Heulin et al., 2007]. This effect of postural characteristics on manual laterality can be easily studied in marsupials since many of them may typically assume both quadrupedal and bipedal posture [Hume et al., 1989; Webster, Dawson, 2003; Dawson, 2012]. In addition, marsupials are characterized by diversity of preferred gaits ranging from fully quadrupedal locomotion to habitual bipedalism [Webster, Dawson, 2003; Kear et al., 2008]. This provides an excellent opportunity to test the hypothesis suggested for primates, which links a pronounced manual laterality with bipedal locomotion [Ward, 1995; Westergaard et al., 1998; Corbetta, 2003]. In the ontogenesis, forelimbs of marsupials develop much earlier than forelimbs of most placentals [Cooper, Stepan, 2010]. In some marsupial species (e.g., members of the family Macropodidae), even pouch young display a considerable manual dexterity [Dawson, 2012]. Therefore, marsupials represent an excellent group to investigate early expression of manual laterality.

In this work, we investigated forelimb preferences in seven species of marsupials (three species were studied in the wild) in a variety of natural behaviours, and generate conclusions regarding the lateralisation of forelimb use in the marsupials studied to date. Unimanual behaviour were studied in grey short-tailed opossum, *Monodelphis domestica* (Didelphidae, Didelphimorphia), sugar glider, *Petaurus breviceps* (Petauridae, Diprotodontia), Goodfellow's tree kangaroo, *Dendrolagus goodfellowi* (Macropodidae, Diprotodontia), red-necked wallaby, *Macropus (Notamacropus) rufogriseus* (Macropodidae, Diprotodontia), eastern grey kangaroo, *M. (M.) giganteus* (Macropodidae, Diprotodontia), red kangaroo, *M. (Osphranter) rufus* (Macropodidae, Diprotodontia), and brush-tailed bettong, *Bettongia penicillata* (Potoroidae, Diprotodontia). In each species manual preferences were studied for at least four behaviours. The effect of sex, age, type of behaviour and body posture (quadrupedal/bipedal) on manual laterality was assessed. Using an observational approach we examined forelimb preferences in natural, not artificially evoked, routine behaviour of captive and wild marsupials. Statistical methods used for data analysis are those commonly used in studies of manual preferences in vertebrates [e.g., Strauss, Wada, 1983; Westergaard et al., 1998; Hopkins et al., 2011; Meguerditchian et al., 2012]. Remarkable similarities between manual lateralisation in primates and marsupials were revealed. Similarities such as: the association between postural characteristics and manifestation of forelimb preferences; the division of functions between the forelimbs; and, the expression of lateralised forelimb usage early in life. The monograph is partly based on the results of our previously published research [Giljov et al., 2012a, b, c, d; 2013; 2015a; 2017; Giljov, Karenina, 2012; Giljov, 2014].

CURRENT KNOWLEDGE OF MANUAL LATERALITY

1.1. Hemispheric asymmetry and behavioural lateralisation in vertebrates

Asymmetry is a key principle of the functioning of the paired brain [Bianki, 1989]. A discovery that paved the way for our understanding of the asymmetrical structure and functioning of the brain was made in the second half of the 19th century by Paul Broca, a French physician and neurologist. Broca found that the loss of ability to produce articulate speech in a patient was due to the damage in a certain area of the left hemisphere of the brain (cit. ex: Lokhorst [1996]). For the sake of fairness, it should be noted that Marc Dax, another French neurologist, discovered the connection between speech impairment and the damage of the left hemisphere almost twenty years before Broca's discovery (cit. ex: Cubelli, Montagna [1994]). Carl Wernicke showed that the left hemisphere was responsible not only for the production of speech but also for the ability to understand it [Wernicke, 1874]. The principle of asymmetry was later found to be expressed in numerous other functions of the human brain besides speech [Brancucci et al., 2009].

Until the early 21st century it was generally considered that only humans possess functional brain asymmetry [Warren, 1980; Crow, 2004]. Textbooks on neurology and psychology postulated that asymmetrical distribution of functions between the right and the left hemispheres was a uniquely human feature, possibly associated with our superior cognitive abilities. The first reports of hemispheric asymmetries in other species were severely criticized if not outright ignored (reviewed in MacNeilage [1993]; Vallortigara et al. [2011]).

The turning point came in the 1970–1980s, when several studies provided compelling evidence of the asymmetrical functioning of the nervous system in several vertebrate species. Fernando Nottebohm and his colleagues [Nottebohm et al., 1976] reported that song in the canary, *Serinus canaria*, was mainly controlled by the left hemisphere. Lateralisation of various brain functions was demonstrated in domestic chicks, *Gallus gallus domesticus* [Rogers, Anson, 1979] and brown rats, *Rattus norvegicus* [Denenberg, 1981] by placement of unilateral lesions or temporary pharmacological blockade of one or the other hemisphere. Vsevolod L. Bianki described the laws of manifestations of brain asymmetry in animals. On the basis of numerous experiments, he suggested a synthetic inductive-deductive hypothesis of the lateral specialisation of the brain [Bianki, 1985]. According to this hypothesis, the right hemisphere mainly performs the deductive processing of information (synthesising it first and analysing it second), while the left hemisphere mainly performs inductive processes (analysis and then synthesis). A synthetic dominance model of interhemispheric relations [Bianki, 1989] provided the inductive-deductive hypothesis of lateral specialisation with a morpho-functional

basis, suggesting that the left hemisphere “develops” a behavioural strategy by using induction, while the right hemisphere applies this strategy using deduction. Bianki generalised the characteristic features of functioning of the left and the right hemispheres, and made an important conclusion that functional specialisation of a hemisphere is not absolute. In other words, both hemispheres can perform a function but one of them takes up the dominant role (one or the other, depending on the task) [Bianki, 1985; 1989]. Recent studies have shown that hemispheric asymmetry is dynamic [Fokin, 2007; Chervyakov, Fokin, 2008]. Hemispheric dominance may shift as a result of a change in the functional state, e.g., during transition from comfort to stress [Fokin, Ponomareva, 2004; Fokin, 2007].

These ground-breaking studies of functional lateralisation in the vertebrate brain provided an impulse for an intensive accumulation of information in the decades that followed. By now, brain asymmetry and associated lateralised behaviour have been studied in many vertebrate species from various taxonomic groups [Vallortigara et al., 2011]. The term “behavioural lateralisation” (or lateralised behaviour) usually refers to the left/right tendencies in the behavioural reactions of animals such as the preference of one limb over the other for certain tasks or a more pronounced reaction to a stimulus presented in the field of vision of an eye [Rogers, 2002; Rogers et al., 2013]. Bony fish, birds and primates are the model taxa in which brain asymmetry and behavioural lateralisation have been studied most comprehensively and in most detail [Halpern et al., 2005]. Numerous studies, both experimental and based on behavioural observations of animals in nature, indicate that brain asymmetry and lateralised behaviour are fundamental traits of vertebrates [Andrew, Rogers, 2002; Vallortigara, Rogers, 2005]. The accumulated evidence is summarised in several reviews highlighting widespread occurrence and diverse manifestations of functional lateralisation of the vertebrate brain [Bisazza et al., 1998; Rogers, 2002; MacNeilage et al., 2009; Tommasi, 2009; Vallortigara et al., 2011; Ströckens et al., 2013]. Recent works indicate that behavioural and functional lateralisation of the nervous system is also common in various groups of invertebrates [Malashichev, 2006a; Downes et al., 2012; Frasnelli et al., 2012; Frasnelli et al., 2014].

Widespread occurrence of the principle of asymmetry in the functioning of the animal brain apparently stems from the advantages of the uneven contribution of the hemispheres in the performance of certain functions [Regolin et al., 2013]. It is thought that the hemispheric specialisation on the performance of certain tasks makes it possible to avoid, at least in part, the duplication of the same functions in both hemispheres [Levy, 1977]. An important advantage of a lateralised brain is the possibility of parallel processing of diverse kinds of information, which, in turn, allows an efficient performance of simultaneous tasks [Vallortigara, Rogers, 2005]. It has been proven experimentally that lateralised individuals are more efficient than non-lateralised ones in situations requiring simultaneous performance of two different types of tasks, e.g., finding food and avoiding predators [Rogers et al., 2004; Dadda, Bisazza, 2006]. Functional asymmetry increases the efficiency of brain function as it enables simultaneous processing of information about various stimuli by task division between the hemispheres. From the viewpoint of general energy processes of an organism, brain asymmetry translates into a decrease in the general growth of the entropy level and the regulation of energy homeostasis [Chernisheva, 2003, 2006].

At present, studies of lateralisation in animal behaviour are usually carried out in one of the two directions: laterality of sensory functions and laterality of motor functions. Sensory laterality is usually defined as a functional asymmetry of sensory organs and the unequal receptiveness to stimuli from the right and the left side of the body associated with it [Bragina,

Dobrokhotova, 1981; Rogers, 2009]. In many cases sensory laterality — visual, auditory or olfactory — is expressed as a preferred use or advantage of the left or the right sensory organ out of a pair [Rogers, 2002]. Lateralisation of visual perception has been studied best so far. Visual laterality, reported for bony fish, amphibians, reptiles, birds and mammals [Vallortigara et al., 2011], is expressed during perception of various types of stimuli such as social partners [Salva et al., 2012], food objects [Robins, Rogers, 2006a], predator [Lippolis et al., 2002] or spatial cues [Rashid, Andrew, 1989].

The lateralisation of motor functions is defined as an unequal participation of the right and the left body side in movement [Hook, 2004; Leutin, Nikolaeva, 2005; Rogers, 2009]. Motor laterality, typical of many vertebrate species [Hook, 2004], may be expressed in the asymmetrical turns of the body [Krylov et al., 2008; Dodson et al., 1992] or the asymmetrical use of paired limbs [Ströckens et al., 2013]. Its manifestations vary considerably not only in different species but even in the same individuals depending of the action performed [MacNeilage, 2007].

1.2. Lateralised limb use in vertebrates

1.2.1. Human handedness and lateralised forelimb use in other species

The best-known example of manual laterality is human handedness [Coren, Porac, 1977]. A considerable majority of people demonstrate right-hand preference [Perelle, Ehrman, 1994; Annett, 2002]. Prehistoric evidence such as artefacts and fossilised remains suggest that right-handed individuals also predominated in other *Homo* species such as *Homo neanderthalensis* and *Homo heidelbergensis* [Uomini, 2009]. However, the proportion of left-handers and right-handers in the human population is subject to geographic variation [Faurie et al., 2005]. A review of 81 published studies of handedness has shown that the proportion of left-handers varies from 5 to 26% in 14 countries of Asia, Europe, America, and Australia [Raymond, Pontier, 2004]. The manifestation of human right-handedness also depends on the character of the motor tasks. Right-hand preference is most strongly expressed for complex actions requiring fine coordination whereas in simple daily actions the right-hand bias is relatively weak [Marchant et al., 1995].

In humans, the preferred hand is stronger, more dexterous and more capable of fine motor coordination than the other one [Bragina, Dobrokhotova, 1981]. However, it would be a mistake to think that the preferred hand dominates completely over the other hand in motor activities [Leutin, Nikolaeva, 2005]. Hand use is usually characterised by complementary role differentiation: one hand performs actions requiring fine spatial and temporal coordination while the other one performs complementary, supportive actions [Corbetta, Thelen, 1996]. Hand use during sewing is an example: one hand performs fine movements, doing the actual sewing, and the other hand takes up an accessory role, keeping the fabric in the correct position. Therefore, there is a division of functions between the two hands rather than a dominance of one hand over the other. Interestingly, the use of the left and the right hand for different tasks is expressed not only in bimanual actions (i.e. actions with simultaneous participation of both hands) but also in unimanual activities involving only one hand [Llaurens et al., 2009]. The most common type of complementary role differentiation between the hands is that during which the right hand mainly performs fine manipulations, and the left hand is used for static efforts such as postural support or holding of objects [Luneva, 1976; Guiard,

1987]. Besides, right-handers were shown to perform open-loop ballistic aimed movements more accurately when using the left rather than the right hand because these movements are finished before the sensory input has been processed [Guiard et al., 1983]. To sum up, the accumulated body of evidence indicates that human handedness is a complex and multidimensional phenomenon, and approaches to its assessment and views on its mechanism and evolution are still highly debatable [Gutnik et al., 2009].

It is still argued whether lateralised limb use by vertebrates other than humans may be as strong and stable as human handedness [MacNeilage, 1993; Rogers, 2009]. However, it is now longer doubted that a more or less marked lateralised limb use is not a uniquely human trait but a feature shared by all vertebrates [Hook, 2004; Ströckens et al., 2013]. In studies of limb laterality in animals the terms “limb preference” or “manual preference” are usually used, implying the preferred use of one limbs for a certain task [Fagot, Vauclair, 1991]. Similarly to other kinds of laterality, manual laterality may be manifested at the individual level (that is, in some individuals of a species) and/or at the populational (group) level (that is, when the same direction of limb preferences is observed in a considerable majority of individuals in a population or a group under study) [Bianki, 1989; Rogers, 2002]. A recent review summarising almost all the available data on lateralised use of limbs [Ströckens et al., 2013] shows that about a half (51%) of the 119 studied species demonstrate limb preference both at the individual and at the population level. In the remaining half of the studied species, 18% demonstrate only individual manual preferences and the remaining 32% demonstrate no lateralised limb use in the studied behaviours.

It is often thought that lateralised limb use is a manifestation of functional lateralisation of the brain [Fagot, Vauclair, 1991; Rogers, 2009]. Connections between the governing and the subordinate systems of an organism may be organised ipsilaterally or contralaterally [Geodakyan, 1993]. Motor activity is controlled contralaterally, i.e. the right hemisphere controls the movements of the left side of the body and vice versa. The connection between hemispheric asymmetry and motor laterality has often been shown for humans and other primates [Geschwind, Galaburda, 1987; White et al., 1994; Rogers, 2009]. In the common chimpanzee, *Pan troglodytes* [Hopkins et al., 2007], the brown capuchin monkey, *Cebus apella* [Phillips et al., 2005] and the squirrel monkey, *Saimiri sciureus* [Nudo et al., 1992] the structural asymmetry of the motor cortex correlates with manual laterality. For instance, in right-handed squirrel monkeys the forelimb representations in the left hemisphere are greater in number, larger in total area and have a greater spatial complexity than in the right hemisphere, whereas in left-handers the opposite pattern is observed [Nudo et al., 1992]. It was found with the use of magnetic resonance imaging that in chimpanzees, which as a species demonstrate a population-level right-hand preference [Hopkins et al., 2011; Llorente et al., 2011], the region of the motor cortex responsible for coordination of the hand movements was greater in the left brain hemisphere [Hopkins, Pilcher, 2001]. Besides, a positive correlation was found between the expression of morphological interhemispheric asymmetry and the strength of manual preferences [Dadda et al., 2006; Hopkins, Nir, 2010].

The advantages of manual laterality are very poorly studied. In cats the preferred paw has a shorter reaction time and a shorter movement time than the less-used paw, and is also more accurate [Fabre-Thorpe et al., 1993; Lorincz, Fabre-Thorpe, 1996]. Among primates an increased efficiency of movements of the preferred hand as compared with the non-preferred one is shown for humans [Flindall et al., 2013] and bonnet macaques, *Macaca radiata* [Mangalam et al., 2014]. Common chimpanzees with a hand preference perform complex unimanual actions more effectively than individuals with no preference [Marchant, McGrew,

1999]. Similar results were obtained on several parrot species: parrots that used their feet asymmetrically outperformed less strongly lateralised individuals in manipulation tasks [Magat, Brown, 2009]. A potential adaptive significance of manual laterality, composed of the increased effectiveness of actions and decreased time expenditure for coordination and movement initiation, might explain the widespread occurrence of limb laterality in vertebrates [Papademetriou et al., 2005; Magat, Brown, 2009].

1.2.2. Occurrence of lateralised limb use in non-mammalian vertebrates

Lateralised limb use is known for bony fish, amphibians, reptiles, birds and mammals. Limb preferences in some vertebrate classes, such as birds and mammals, are studied in much detail and on many species, whereas other classes have mostly been ignored. Here we discuss only the most relevant studies on various vertebrate groups, highlighting the widespread occurrence of limb laterality and the diversity of its manifestations. The results of studies on mammals will be discussed separately in section 1.2.3.

Bony fish (*Osteichthyes*). Preferences in the use of paired fins are known for two species of bony fish. Channel catfish, *Ictalurus punctatus* can produce sound using spines (modified first rays of the pectoral fins) [Ladich, Fine, 1994]. A half of individuals in the studied sample prefer to produce sounds with one of the spines, with most of the lateralised catfish preferring the right spine [Fine et al., 1996]. Lateralised movements of modified ventral fins during tactile exploration of space were studied in the blue gourami, *Trichogaster trichopterus*. During initial exploration of novel plastic objects the gourami showed left-fin preference at the population level [Bisazza et al., 2001]. It remains unknown, however, whether fin preferences in fish and limb preferences in tetrapods are associated with similar mechanisms.

Amphibians (*Amphibia*). Lateralised limb use has been studied only in anuran amphibians (Anura) [Ströckens et al., 2013]. A common technique for studying limb preference in anurans is a snout-wiping test, registering which of the forepaws the animal uses to wipe off a foreign object (e.g., a strip of paper or a piece of plastic) off the snout [Bisazza et al., 1996]. In this test, common toads, *Bufo bufo* [Bisazza et al., 1996] and green tree frogs, *Litoria caerulea* [Malashichev, 2006b] demonstrated group-level preference of the right forepaw, while European green toads, *B. viridis* [Bisazza et al., 1996], common spadefoot toads, *Pelobates fuscus*, ornate horned frogs, *Ceratophrys ornata* [Malashichev, 2006b], oriental fire-bellied toads, *Bombina orientalis* [Goree, Wassersug, 2001] and fire-bellied toads, *B. bombina* [Malashichev, Nikitina, 2002] did not show any statistically significant group-level preference.

In another experiment, anuran amphibians were turned onto their backs and the researcher registered which of the limbs was used to pivot the body into the righting position (“righting task”) [Bisazza et al., 1996, 1997]. In the righting task, common spadefoot toads [Malashichev, 2006b], common toads and cane toads, *B. marinus* [Robins et al., 1998] demonstrated group-level preference of the right hind paw, while European green toads [Malashichev, Nikitina, 2002] and ornate horned frogs [Malashichev, 2006b] preferred the left hind paw. Green tree frogs preferred to perform the righting task with the right forepaw [Robins, Rogers, 2006b]. Clawed frogs, *Xenopus laevis* demonstrated no paw preference for turning the body when diving after surfacing to breathe [Kostylev, Malashichev, 2007].

To conclude, lateralised use of forelimbs and/or hind limbs is characteristic of some anuran species, whereas some other species demonstrate no lateralisation for the studied actions. The direction of preferences may vary even in congeneric species.

Reptiles (Reptilia). Lateralised use of limbs by reptiles has been studied only in Testudines (turtles and tortoises). In a righting test, Hermann's tortoises, *Testudo hermanni* positioned upside-down demonstrated a group-level preference of the right forelimb and the right hind limb for uprighting [Stancher et al., 2006]. A similar study involving two species of turtles, the green turtle, *Chelonia mydas* and the olive ridley turtle, *Lepidochelys olivacea* demonstrated both individual and group-level preference for the use of the right limbs for self-righting. These, however, were weaker than in Hermann's tortoises, possibly due to the differences in locomotion: while turtles swim by synchronous strokes of all the four flippers, land tortoises move by asynchronous (alternating-limb) walking [Malashichev, 2016].

In leatherback turtles, *Dermochelys coriacea*, lateralised limb use was studied by observing their natural behaviour in the wild. It was found that nesting leatherback turtles usually cover the egg chamber during oviposition with the right hind flipper [Sieg et al., 2010]. However, this "flipperedness" was observed only in the analysis of the total number of cases of the left and the right hind flipper use for all the studied turtles, whereas individual preferences were repeatedly found only in two individuals. A peculiar method of data collecting and processing employed in that study does not allow a direct comparison of the data on lateralised limb use in leatherback turtles and other vertebrate species [Ströckens et al., 2013]. However, a rather weakly expressed "flipperedness" of leatherback turtles agrees well with the hypothesis about the role of synchronous locomotion in the disappearance of a marked motor asymmetry in the evolution of sea turtles [Malashichev, 2016].

Birds (Aves). As far as limb preferences are concerned, birds are one of the best studied groups of vertebrates. Parrots (Psittaciformes) were the first birds to be studied in respect of motor preferences [Harris, 1989]. William Ogle observed the behaviour of several parrot species in the London Zoo and showed that these birds preferred to manipulate food with the left foot [Ogle, 1871]. These observations inspired studies of lateralised feeding behaviour in other parrot species. In the 20th century, foot laterality in parrots remained in the focus of laterality studies [Giljov et al., 2011]. By now, lateralised use of feet has been studied in 32 parrot species. Seven of them demonstrate no foot preferences; three species demonstrate preferences only at the individual level, while 19 species demonstrate a marked laterality both at the individual and at the population level [Ströckens et al., 2013]. Out of 19 species showing the population-level laterality, in 13 species most individuals prefer to manipulate food with their left foot, while in six species most individuals are right-footed. The expression of foot preferences in parrots was shown to be associated with the species-specific character of feeding: laterality is more characteristic of species feeding on large food items such as fruit, nuts etc. than for those feeding on small seeds or flowers [Brown and Magat, 2011b]. This may be due to the fact that the former frequently have to manipulate food, whereas the latter do not need to do so.

Footedness has also been investigated in representatives of some other avian groups besides parrots. Foot-use preferences were studied experimentally in jungle crows, *Corvus macrorhynchos* (Passeriformes). A considerable majority of the crows demonstrated stable individual foot preferences for beak-scratching but no group-level bias was found [Izawa et al., 2005]. Footedness was also examined in three species of Galliformes. Domestic chicks, *Gallus gallus* showed a population-level right-foot preference for removing a piece of adhesive tape in a beak-scratching experiment [Rogers, Workman, 1993], and for starting locomotion forwards [Casey, Martino, 2000]. The right foot is the starting foot, too, in the northern bobwhite, *Colinus virginianus* [Casey, 2005]. At the same time, the Japanese quail, *Coturnix japonica* showed no foot preferences for starting locomotion forwards [Casey, 2005]. In

ostriches, *Struthio camelus* (Struthioniformes) right-foot preference for starting locomotion forwards was found at the population level [Baciadonna et al., 2010]. It may be associated with the lateralised behaviour during hatching: ostrich chicks typically use the right foot to break the egg shell [Cooper, 2001].

In a large-scale study of foot preferences in wildfowl and waders, Christophe Randler observed 4646 birds from 25 species roosting on the ground on one foot during migration stopover [Randler, 2007]. He found that four species — the avocet, *Recurvirostra avosetta*, the northern shoveller, *Anas clypeata*, the oystercatcher, *Haematopus ostralegus* and the Eurasian curlew, *Numenius arquata* — preferred to rest standing on the right foot, while 21 species showed no lateralisation in this behaviour [Randler, 2007]. Captive northern bald ibises, *Geronticus eremita* showed a group-level preference for perching on the right foot and scratching with the left one [Anderson, Robinson, 2012].

A study of lateralised feet use during hunting in Falconiformes and Strigiformes showed that kestrels, *Falco tinnunculus*, buzzards, *Buteo buteo* and barn owls, *Tyto alba* grasped the prey predominantly with the right foot [Csermely, 2004].

Several studies on birds revealed a link between the foot preference and brain functioning. African grey parrots, *Psittacus erithacus* preferring the right foot for feeding have larger lexicons than left-footed individuals [Snyder, Harris, 1997]. Lateralised foot use in parrots was shown to be associated with visual asymmetry: the preference to use the left or the right foot correlated with the preference to scrutinize the manipulated object with the ipsilateral eye [Brown, Magat, 2011a]. The same authors found that in eight parrot species lateralised (left-footed and right-footed) individuals were more successful in solving experimental food-obtaining tasks than non-lateralised ones [Magat, Brown, 2009]. It has been suggested that a marked cerebral lateralisation (manifested in lateralised foot use) in birds enhances cognitive functions of the brain [Magat, Brown, 2009].

1.2.3. Forelimb laterality in mammals

The number of mammals (Mammalia) for which lateralised limb use has been reported is quite high but most of them are primates. Other mammal groups have not been studied in a comprehensive and detailed manner. Manual laterality in marsupials (Marsupialia) and monotremes (Monotremata) has until recently remained an unknown territory.

In rodents (Rodentia), motor preferences were first studied in house mice, *Mus musculus*: mice presented with a task to retrieve food in a specially devised test apparatus showed individual but not population-level paw preferences [Collins, 1968]. However, these results were later contested: under other experimental conditions mice demonstrated a statistically significant right-paw preference at the population level [Bianki, 1985; Waters, Denenberg, 1994]. The dominance of the left hemisphere in the control of motor activity in mice was shown in one study [Bianki, 1985] but not supported in another one [Mikheev, Shabanov, 2009]. Some of the discrepancies between the experimental results of motor asymmetry studies in mice may be associated with the use of different strains of mice [Mikheev, Shabanov, 2009].

Right-pawed individuals predominated in two isolated urban populations of the striped field mouse, *Apodemus agrarius* [Agulova et al., 2010]. Population-level right-paw preference for manipulating food objects under experimental conditions was also reported for brown rats, *Rattus norvegicus* [Güven et al., 2003]. Another study indicated that paw preferences for food-reaching tasks were formed in rats in the course of the learning process, whereas initially no

lateralised use of paws was present [Stashkevich, 2009]. Male rats — both right-pawed and left-pawed — performed the actions more precisely with the preferred paw when reaching for food pellets from a narrow cylinder [Stashkevich, 2013]. Besides, right-pawed and left-pawed rats showed some differences in the characteristics of the learning process [Stashkevich, 2009]. In Mongolian gerbils, *Meriones unguiculatus*, the direction of laterality depended on the sex: in the tripod stance (i.e. resting on both hind paws and one forepaw) the males preferred to support the body with the right forepaw, while the females preferred the left one [Clark et al., 1993]. Interestingly, in an “open field” test male Mongolian gerbils more often turn to the right while the females turn more often to the left [Morenkov, 2004]. It is unknown whether paw preferences during resting in the tripod stance are linked to the predominant direction of turns.

Data on manual laterality in carnivores (Carnivora) are contradictory in many respects. After various tests, Glumov [1984] concluded that most of the cats, *Felis silvestris catus* in his study demonstrated a right-paw preference. In another study, cats trained to perform a reaching movement towards a moving target demonstrated a group-level left paw preference [Fabre-Thorpe et al., 1993]. In a food-reaching test, where food could be retrieved from a narrow cylinder using one of the forepaws, cats showed marked individual preferences but no group bias [Pike, Maitland, 1997]. In a similar test involving retrieval of food from a cylinder as well as reaching for a moving object, paw preferences in cats were found to depend on sex: males were more inclined to use the left paw while females tended to use the right paw [Wells, Millsopp, 2009]. Movements made by a more-used paw are quicker and more accurate than those made by the other paw regardless of the direction of the preference [Fabre-Thorpe et al., 1993; Lorincz, Fabre-Thorpe, 1996].

Functional paw preferences were studied in lions, *Panthera leo*. Observations on the behaviour of captive lions showed that most of them preferred to manipulate objects using the right forepaw [Zucca et al., 2011a]. The same study found that the lateralised use of forepaws was influenced by health conditions: the strength of laterality, i.e. the expression of the preference regardless of its direction, was lower in healthy animals.

Paw preferences in dogs, *Canis familiaris* were studied in various behaviours. In two independent studies on large samples of dogs of various breeds ($n = 53$ [Wells, 2003]; $n = 80$ [Quaranta et al., 2004]), most individuals showed individual paw preferences but no population-level laterality was observed. The direction of preferences when the paw was used to remove an object from the snout [Quaranta et al., 2004], to retrieve food from a can and to perform the “give a paw” task [Wells, 2003] was associated with sex: female dogs preferentially used the right paw while male dogs preferred to use the left paw.

In the wild, limb preferences in carnivorous mammals were observed in wild black bears, *Ursus americanus kermodei* [Reimchen, Spoljaric, 2011] and Atlantic walrus, *Odobenus rosmarus rosmarus* [Levermann et al., 2003]. Both species showed the right forelimb preference during feeding.

Functional forelimb preferences were investigated in several species of even-toed (Artiodactyla) and odd-toed (Perissodactyla) ungulates [Ströckens et al., 2013]. Using their forelegs to uncover subnivean forages during winter, muskoxen, *Ovibos moschatus* did not show any individual or group-level laterality [Schaeffer, Messier, 1997], whereas most studied domesticated reindeer preferred to use the left foreleg [Espmark, Kinderas, 2002]. In feral horses, *Equus ferus caballus* preferences to place one forelimb in front of the other during grazing were studied. No population-level laterality was found, although some individuals demonstrated a stable preference to place one forelimb in front of the other [Austin, Rogers, 2012].

In bats (Chiroptera), motor laterality was studied in Schreiber's long-fingered bats, *Miniopterus schreibersii*. When climbing on vertical walls of a plastic cylinder in experiment, most individuals preferred to use the left hand [Zucca et al., 2010].

Lateralised limb use was also recorded in cetaceans (Cetacea). Observations on the behaviour of humpback whales, *Megaptera novaeangliae* [Clapham et al., 1995] and orcas, *Orcinus orca* [Giljov et al., 2016] showed that during flippering these animals slapped the water surface with the right flipper considerably more often than with the left one. Wild Indo-Pacific bottlenose dolphins, *Tursiops aduncus* preferred to use the left flipper for tactile interactions with conspecifics but showed no laterality in the use of flippers during the object-carrying behaviour [Sakai et al., 2006]. However, the asymmetry observed during social contacts between the bottlenose dolphins appears to be a side effect of their preference to keep the social partner in view using the left eye rather than an effect of motor asymmetry as such.

Without any doubt, primates (Primates) are the best studied group of mammals as far as limb preferences are concerned, and humans are the best studied primates. Manual laterality in humans was studied in diverse types of motor activity [Marchant et al., 1995], in different ethnic groups [Raymond, Pontier, 2004] and in various historical periods [Harris, 1980; Annett, 2002; Uomini, 2009]. It should be noted that many studies tended to overestimate the degree of expression of right-handedness in humans [Perelle, Ehrman, 1994; Annett, 2002]. This was associated with the use of questionnaires and tests aimed at revealing the hand preference in actions requiring fine motor skills such as writing [Vallortigara et al., 2011]. A study of object manipulation in African and South American traditional societies from preliterate cultures showed that in daily activities humans from these societies showed only a weak individual right-hand dominance, with the proportion of left-handers to right-handers being approximately 45:55 [Marchant et al., 1995]. The only exception was the instrumental handling of an object: most people performed fine-motor manipulations of tools mainly or exclusively with the right hand.

Manual preferences of primates are usually studied during feeding: it is registered how often the animal uses the left or the right hand to reach for a food object and to bring it to the mouth. Hand preferences for feeding were studied in 15 species of Strepsirrhini [Ströckens et al., 2013]. Left-handers dominated in the studied samples in 11 species, e.g. black and white ruffed lemurs, *Varecia variegata variegata* [Nelson et al., 2009] and northern greater galago, *Otolemur garnettii* [Ward, Cantalupo, 1997]. In other studied species of Strepsirrhini, e.g., grey mouse lemurs, *Microcebus murinus* [Scheumann et al., 2011] and aye-ayes, *Daubentonia madagascariensis* [Lhota et al., 2009] only individual manual preferences were observed but no group-level laterality was found.

Within the Haplorhini, some species display the left preference, e.g., squirrel monkeys, *Saimiri sciureus* [King, Landau, 1993], species biased towards the use of the right hand, e.g., brown capuchin monkeys, *Cebus apella* [Westergaard, Suomi, 1993] and species with no population-level bias in manual preferences for feeding, e.g., marmosets, *Callithrix jacchus* [De Sousa et al., 2001]. Manual laterality can differ even in congeners. Most Japanese macaques, *Macaca fuscata* [Kubota, 1990], rhesus monkeys, *M. mulatta*, and pigtail macaques, *M. nemestrina* [Westergaard et al., 2001] preferred to reach for food with the left hand, while cynomolgus monkeys, *M. fascicularis* [Westergaard et al., 2001], Barbary macaques, *M. sylvanus* [Schmitt et al., 2008] and moor macaques, *M. maura* [Watanabe, 2010] did not show any group-level laterality. Studies on rhesus monkeys showed that the use of the preferred hand in an instrumental task is characterised by a lesser latent period of

the motor response and a faster maximum speed of movements [Tereshchenko et al., 2012].

A common method of assessing hand preferences in primates is the “tube task”, in which an animal has to extract food out of a narrow cylinder [Hopkins, 1995]. In contrast to other common measures of hand use, the “tube task” requires simultaneous participation of both forelimbs: the animal holds the tube with one hand and extracts food with the other one. This bimanual task is generally acknowledged to be a more consistent and reliable test for assessing hand preferences in primates than the usual feeding [Canteloup et al., 2013; Meguerditchian et al., 2013]. William D. Hopkins and colleagues conducted a large-scale study of lateralisation for the “tube task” in orangutans, *Pongo pygmaeus* ($n = 47$), gorillas, *Gorilla gorilla* ($n = 76$), chimpanzees, *Pan troglodytes* ($n = 536$), and bonobos, *Pan paniscus* ($n = 118$) in captivity [Hopkins et al., 2011]. They found population-level right-handedness in gorillas, chimpanzees and bonobos and population-level left-handedness in orangutans [Hopkins et al., 2011]. In nature, manual laterality for a bimanual task was studied in one primate species, Sichuan snub-nosed monkeys, *Rhinopithecus roxellana*. Tubes with food inside were left for monkeys at provisioning sites [Zhao et al., 2012]. All the subjects showed strong individual hand preferences, with most of them preferring the left hand for food extraction.

Contradictory results of some of the earlier studies of handedness in primates made the scientific community distrustful of the works demonstrating a marked population-level motor preference in any animal species [Rogers, 2009; Vallortigara et al., 2011]. A number of studies reproducing previous research were carried out to check the validity of the results. In one such instance, laterality for bimanual actions in chimpanzees and gorillas was studied with the use of the same method by two research teams. Both in chimpanzees [Hopkins, 1995; Llorente et al., 2011] and in gorillas [Meguerditchian et al., 2010; Tabiowo, Forrester, 2013] the right-hand preference at the population level was independently confirmed.

Lateralisation for the “tube task” and other bimanual actions indicates that handedness, at least for high-level manipulative actions, is not a uniquely human trait but is also characteristic of other primates [Hopkins et al., 2011]. Noteworthy, the direction of the population-level laterality for bimanual activity is similar in humans, chimpanzee, bonobos and gorillas [Meguerditchian et al., 2013]. Right-handedness for complex manipulations is thought to be linked with the left hemisphere dominance for the control of structured bimanual actions, a feature inherited by humans and other hominins (Homininae) from a common ancestor [Tabiowo, Forrester, 2013].

Manipulations during feeding described above are not the only types of actions in which lateralised limb use has been studied. Hand preferences of primates were also assessed for such tasks as manipulation of non-food objects, touching of conspecifics, self-touch, auto- and allogrooming and offspring carrying [Hopkins, 2006]. Laterality of gestural communication is of special interest for primatologists. Large-scale studies of primates kept in groups in the zoos and laboratories of North America and Europe showed that chimpanzees, bonobos, gorillas and orangutans are right-handed for gestural communication [Hopkins et al., 2012]. In all these species, right-handedness for manual gestures was expressed more strongly than for movements not associated with communication [Meguerditchian et al., 2013]. Besides, auditory gestures (e.g., clapping) were more lateralised than visual and tactile ones. An enhanced right-hand preference for gestural communication is thought to be associated with the dominance of the left hemisphere for communicative functions [Hopkins et al., 2012]. The lateralisation of auditory gesticulation in primates might have been the precursor of the left hemisphere specialisation for speech functions in humans [Meguerditchian et al., 2013].

An overwhelming majority of studies of lateralised motor functions in primates focus on manual preferences but a study by Dapeng Zhao and his colleagues [Zhao et al., 2008b] indicates that primates may have foot preferences as well. Wild Sichuan snub-nosed monkeys showed an individual preference to initiate locomotion with the left or the right foot. No group-level bias was observed but foot preference in all individuals was stronger for bipedal locomotion than for quadrupedal locomotion [Zhao et al., 2008b]. Humans show a population-level foot preference: in most people the right foot plays the active role (initiates walking [Seltzer et al., 1990] or is used for interactions with objects such as kicks and pushes [Carey et al., 2009]), while the left foot is mostly used for static postural support [Seltzer et al., 1990].

Until recently lateralised limb use in mammals outside Placentalia has been very poorly studied. In our previous work, we observed four captive individuals of long-beaked echidnas (a male and a female of the western long-beaked echidna, *Zaglossus bruijni* and a male and a female of the eastern long-beaked echidna, *Zaglossus bartoni*) [Giljov et al., 2015b]. The echidnas showed significant forelimb preferences in three types of actions: feeding (holding the food with one forepaw), stepping on an eminence (overcoming an obstacle) and, for males, putting one of the forepaws on the female's back (usually during attempts to push it away from the feeding tray). The two studied males showed individual preferences of the opposite direction across all the three types of actions: while the male of the western long-beaked echidna preferred to use left forelimb, the male of the eastern long-beaked echidna preferred to use the right one. The female of the western long-beaked echidna also preferred to use the left forelimb for feeding. The female of the eastern long-beaked echidna showed some tendency towards the use of the right forelimb but its preferences were not statistically significant [Giljov et al., 2015b]. To date, this is the only report on lateralised use of limbs in monotremes.

Only a very limited number of studies have investigated lateralisation of motor functions in marsupial mammals (Marsupialia). Brush-tailed possums, *Trichosurus vulpecula* [Megirian et al., 1977] and grey short-tailed opossums [Ivanco et al., 1996] demonstrated individual forelimb preferences when reaching for food under experimental conditions. Forelimb preferences in daily activities were examined in ten captive red-necked wallabies, *Macropus (Notamacropus) rufogriseus*. A group-level preference for the left forelimb was found for starting locomotion, self-scratching and postural support, while no significant bias was revealed in food reaching and food pulling [Spiezio et al., 2016].

1.2.4. General approaches to the study of manual preferences

Approaches to the study of limb laterality have undergone fundamental changes in the course of the development of this field of science [Harris, 1989; 1993]. Its main historical stages can be identified by considering, for example, the research conducted on parrots (Psittaciformes), a model group for motor laterality studies [Harris, 1989; Giljov et al., 2011].

Until the middle of the 20th century these studies were mostly descriptive, aiming merely to identify the left or the right foot preference. As there were no methods of assessment of manual preferences at that time, the conclusions were often insufficiently supported by empirical evidence. For instance, William Ogle, an English physician, concluded in his pioneering work on “footedness” in parrots that all parrots were left-footed [Ogle, 1871]. Analysing his own observations on 86 parrots, Ogle failed to take into account the species of the bird. The conclusion about the overall left-footedness of parrots was later refuted [Ströckens et al., 2013].

At the next stage of limb laterality studies, most efforts were devoted to the connection between the morphological asymmetry and the limb preference [McNeil et al., 1971] and the manifestation of limb preference in various taxonomic groups [Rogers, 1980]. In the second half of the 20th century, research priorities shifted to the study of mechanisms underlying lateralised limb use, while systematic accumulation of information about manual preferences in vertebrates continued [Harris, 1989, 1993]. As the number of laboratories specialising on the study of lateralised animal behaviour increased, generally accepted methods of assessing manual preferences were elaborated.

The end of the 20th century witnesses a surge of interest in the adaptive significance of manual preferences and their influence on the interactions of the animal with the environment, and these issues are now considered as promising research directions [Rogers, 2009; Giljov et al., 2011]. Differences in the behaviour of right- and left-handers [Rogers, 2009] and the links between the manifestations of limb preferences and the cognitive functions of an individual [Magat, Brown, 2009] have been studied. An increasing attention is being paid to limb laterality in wild animals [Randler, 2007; Randler et al., 2011; Reimchen, Spoljaric, 2011; Zhao et al., 2012].

1.2.5. Methods of assessing manual preferences: experiment, observations of captive animals, observations of wild animals

The diversity of methods used in studies of motor laterality in vertebrates is steadily growing [Rogers, 2009]. We consider below only the methods which are currently most often used in studies of lateralised limb use in mammals.

Manual preferences in mammals can be studied experimentally or by observation. Experimental studies are usually conducted on captive animals in laboratories or zoos. The easiest and the most common method of assessing manual preferences in primates is the reaching task: an animal offered a small food object reaches for it with the left or the right hand [Ward et al., 1990; Laska, 1996; Meunier, Vauclair, 2007]. For the mammals that are likely to take food with both forelimbs or without resorting to forelimbs at all, the food object is placed into a container with a narrow opening so that it can only be extracted by using a single forelimb [Collins, 1968; Pike, Maitland, 1997; Wells, 2003]. To identify individual preferences, the experiment with one and the same animal is repeated a certain number of times and often in the course of several days.

Such experiments are usually modified in order to study various factors that may potentially influence the manifestation of manual preferences. To assess the effect of the body posture, an experiment with the same individual is conducted in two variants [Westergaard et al., 1998]. In the first variant the food objects are placed at the level of the floor of the cage. In this case, the animal takes up the food from the quadrupedal posture, that is, initially standing on all fours. In the second variant, the food objects are placed above the level of the animal's body. In this case, in order to get the food, the animal has to raise itself on both hind limbs, that is, to assume the bipedal posture. Comparing the expression of laterality in individuals in the quadrupedal and in the bipedal position, one can see if laterality is correlated with postural characteristics [Braccini et al., 2010; Konerding et al., 2012].

Complexity of the manipulation task is another factor often considered in studies of lateralised limb use in mammals. To assess it, manual preferences of an animal are compared in two types of actions: manipulation of non-moving food object, which can be eaten at

once (low-level task), and capture of live moving prey, which requires fine and fast motor coordination (high-level task) [Fagot, Vauclair, 1991]. Food extraction from a container, e.g., when nuts or some other treat are placed in a small cylinder, may also be considered as a high-level task [Hopkins, 2006]. An experimental approach has also been used, albeit rarely, for assessing manual preferences of wild animals. In one study, manual preferences of wild Sichuan snub-nosed monkeys for high-level tasks were assessed by leaving tubes with food at provisioning sites in a national park [Zhao et al., 2012].

The expression of lateralised behaviour in mammals may be influenced by an unfamiliar environment or situation [Chuyan, Gornaya, 2010; Rogers, 2010]. Stress from being placed into an experimental environment may result in a change in the indices of lateralised behaviour [Hopkins, 2006]. For instance, wild redfronted lemurs, *Eulemur ruffifrons* showed stronger individual manual preferences during food extraction from an artificial feeding box (novel situation) than during usual feeding (daily situation) [Schnoell et al., 2014]. Hand preferences of the same individuals of captive aye-ayes differed in the experiment and in spontaneous activities (discussed in Lhota et al. [2009]).

These facts highlight the importance of behavioural observations in studies of manual laterality in mammals. Such observations can be made on both captive and wild animals. Contrary to experimental studies, observations of captive animals aim to minimise the effect of the researcher or other artificial factors on the animal's behaviour. It cannot be always ruled out, however, that information on manual preferences obtained on captive individuals would still deviate from their "natural" preferences.

A general scheme of a study of limb preferences based on behavioural observations of wild animals usually comprises the following stages. 1. Preliminary observations aiming to identify the most common discrete motor actions with the use of one limb (unimanual actions) and the most common discrete motor actions with unequal participation of the two limb (bimanual actions). 2. Observations for the purpose of data collection: registration (usually video recording) of limb use in the studied types of acts; identification of the identity, sex, and age of animals based on their visual characteristics. 3. Processing and analysis of the data: pooling the data obtained from the same individual in different days (sessions) of observations; statistical comparison of actions performed with the left and the right limb from each individual in each types of actions; statistical comparison of the number of left-handers and right-handers in the sample; statistical assessment of the influence of various factors (sex, age, body posture, type of actions etc.) on the preferences. This scheme, with some variations due to characteristics of the subject and the aim of the study, has been used for assessing manual preferences in wild primates of many different species [Boesch, 1991; Marchant, McGrew, 1996; Lonsdorf, Hopkins, 2005; Rigamonti et al., 2005; Zhao et al., 2008a; Lhota et al., 2009; Smith, Thompson, 2011; Schnoell et al., 2014]. To note, the diversity of action types in studies of wild animals is much higher than in studies of captive animals. In wild primates manual preferences have been studied for allogrooming, ant-fishing, nut-cracking, and wadge-dipping [Lonsdorf, Hopkins, 2005], collecting and drinking water from tree holes [Morino, 2011], pulling tree branches [Smith, Thompson, 2011], and supporting the body [Rigamonti et al., 2005].

1.3. Plasticity of manual laterality in mammals

Manual laterality is highly variable. The expression of forelimb preferences may vary considerably within species and between taxonomic groups [Hopkins, 2006; MacNeilage, 2007; Schnoell et al., 2014]. We discuss below the key factors known to influence manual laterality manifestation in different vertebrate species.

1.3.1. Key factors influencing manual laterality within a species

Sex. One of the most frequently studied factors influencing manual laterality is the sex of the individual. Sex was shown to have an effect on manual preferences in many vertebrate species [Bianki, Filippova, 2003; Pfannkuche et al., 2009]. A review of numerous papers on the assessment of sex differences in the manifestation of human handedness demonstrated that left-handers were more common among men than among women [Sommer et al., 2008]. The results of research on various primate species indicate that in general right-handedness is more characteristic of females than of males [Ward, 1995; Corp, Byrne, 2004; Bennett et al., 2008; Llorente et al., 2011; Meguerditchian et al., 2012]. At the same time, no considerable sex differences were found in several studies on primates [Vauclair et al., 2005; Meunier, Vauclair, 2007; Lhota et al., 2009]. In other taxonomic groups stronger differences in the manifestations of motor laterality between the sexes were observed. In horses [McGreevy, Thomson, 2006], Mongolian gerbils [Clark et al., 1993], domestic cats [Wells, Millsopp, 2009] and dogs [Wells, 2003; Quaranta et al., 2004] males and females showed limb preferences of the opposite direction. It had been suggested that sex differences in the expression of laterality in humans and animals might be associated with a differential influence of the hormones on the development and function of the left and the right hemisphere [Geschwind, Galaburda, 1987; Bianki, Filippova, 2003]. However, recent studies do not support this hypothesis [Pfannkuche et al., 2009]. Differences in motor preferences in males and females may be determined by the sex dimorphism in the size of corpus callosum, the main fibre tract connecting the two hemispheres [De Lacoste, Woodward, 1988; Phillips et al., 2007].

Age. Age of an individual may also influence the manifestations of manual laterality. Right-hand bias in humans is manifested already during prenatal development [De Vries et al., 2001]. Until the age of three, the manifestation of handedness is highly variable, and stable hand preference is established only by the age of three to seven [Corbetta, 2003; Leutin, Nikolaeva, 2005]. In humans, a gradual decrease in the strength of hand preference with age is observed, with the hand movements becoming more symmetrical [Kalisch et al., 2006]. In other mammals the effect of age on laterality is highly variable. In cats, *Felis silvestris catus* [Wells, Millsopp, 2012], brown capuchin monkeys, *Cebus apella* [Westergaard, Suomi, 1993], and chimpanzees, *Pan troglodytes* [Hopkins, Fernández-Carriba, 2000] the expression of hand preference becomes stronger with the increasing age of the individual. On the other hand, in several species of lemurs, *Lemur* spp. [Ward et al., 1995] and squirrel monkeys, *Saimiri sciureus* [Laska, 1996] manual laterality is weaker in older individuals than in young ones. In grey mouse lemurs, *Microcebus murinus* [Leliveld et al., 2008], olive baboons, *Papio anubis* [Vauclair et al., 2005], and gorillas, *Gorilla gorilla* [Meguerditchian et al., 2010] no effect of age on manual preferences was found.

Characteristics of actions. The effect of the characteristics of the performed actions on the manual preferences was shown for most vertebrates studied in this respect [Hopkins, 2006;

Schiffner, Srinivasan, 2013; Ströckens et al., 2013]. In some primates, including humans, a division of functions between the forelimbs is present: one hand is mainly used for manipulating objects, whereas the other hand plays the supporting role, maintaining the necessary body posture [Guiard, 1987; Milliken et al., 2005; Hopkins, 2008]. According to the “Postural origins theory”, primates evolved specialisations in limb use in connection with the arboreal way of life: while feeding at a tree branch, early primates have to support the body with one hand and to manipulate food with the other hand [MacNeilage et al., 1987; MacNeilage, 1991].

Complexity of an action may also influence the expression of laterality. Joël Fagot and Jacques Vauclair suggested that “high-level” (complex) tasks elicit a stronger manual preference than simpler low-level tasks [Fagot, Vauclair, 1991]. High-level tasks include actions requiring speed, fine motor coordination, and/or complex sequence of actions, such as seizing live prey, nut-cracking, and tool use. Low-level tasks are simple one-stage actions, such as bringing food that does not have to be processed to the mouth. In many primates the expression of individual and group-level manual preferences increases in high-level tasks as compared to low-level tasks [Boesch, 1991; Westergaard, Suomi, 1996; Lonsdorf, Hopkins, 2005; Hopkins, 2006; Zhao et al., 2012; Schnoell et al., 2014]. For instance, squirrel monkeys displayed left-paw preference for capturing live prey, but when the same individuals reached for pieces of fruit, no group-level paw preference was observed [King, Landau, 1993].

Body posture. The effect of body posture of an individual during performance of actions on the manual preferences was shown in many primate species [Westergaard et al., 1998]. Laterality is usually compared during feeding from the quadrupedal position (standing on all four limbs) and from the bipedal position (standing on both hind limbs). In most studied species the bipedal body posture enhanced lateralisation at the individual and/or at the group level [Hopkins, 1993; Ward et al., 1993; Westergaard et al., 1997; Westergaard et al., 1998; Blois-Heulin et al., 2007; Braccini et al., 2010]. For instance, when chimpanzees reached for food from the quadrupedal posture, distribution of left-handers, right-handers, and individuals without hand preferences was random [Hopkins, 1993]. However, when the same chimpanzees reached for food from the bipedal position, most of them showed individual preferences, and the number of right-handers among the lateralised individuals considerably exceeded that of left-handers [Hopkins, 1993].

It is unknown why lateralisation is stronger in the bipedal posture. It was hypothesised that the differences in manual preferences are caused by differences in the stability of the bipedal and the quadrupedal posture [Ward, 1995]. According to this hypothesis, an unstable bipedal body posture is associated with an increased activation of the nervous system, in particular, the motor brain centres. The excitation of the nervous system may, in turn, result in a stronger expression of motor laterality [Ward, 1995]. This hypothesis, however, fails to explain the absence of stronger manual preferences in the bipedal posture in some species. In such quadrupedal mammals as cats [Konerding et al., 2012], grey mouse lemurs, *Microcebus murinus* [Scheumann et al., 2011], and tree shrews, *Tupaia belangeri* [Joly et al., 2012] a forced bipedal position did not result in any changes in paw preference as compared with the usual quadrupedal position. At the same time, in humans, a species with balanced bipedalism [Skoyles, 2006; Niemitz, 2010], hand preference is equally strong in the (non-typical) quadrupedal body position and the (usual) bipedal posture [Westergaard et al., 1998]. This indicates that body posture influences laterality in a different way in different mammals.

Conditions. Most of the studies of manual preferences in mammals have been made on captive animals [Ströckens et al., 2013]. It has often been noted that artificial conditions cre-

ated for animals in captivity may considerably influence the manifestations of manual laterality [McGrew, Marchant, 1997]. A study of forelimb preferences in donkeys, *Equus asinus* in zoos showed that space availability had an effect on lateralization [Zucca et al., 2011b]. The proportion of left- and right-handers among gorillas born in captivity and those born in the wild (but kept in captivity) was significantly different [Hopkins, 2006]. Population-level laterality of some manual functions differs considerably in wild and captive chimpanzees [Marchant, McGrew, 1996]. Besides, mother-reared captive chimpanzees showed stronger hand preferences than nursery-reared ones [Hopkins, 1994]. In wild-caught chimpanzees, right-handedness was weaker than in captive-born ones [Hopkins et al., 2003], but, at the same time, right-hand preference for certain tasks was stronger in wild-caught chimpanzee than in chimpanzees studied in captivity [Hopkins et al., 2007].

However, in a number of studies wild animals displayed weaker manual preferences than animals studied experimentally or observed in captivity [Marchant, McGrew, 1996; Mittra et al., 1997; Randler et al., 2011]. The reason may be that in the complex, often asymmetrical natural environment the animal does not always get a chance to use the preferred limb. Captive conditions, in contrast, are characterised by relatively uniform environment, which do not prevent the use of the preferred limb [Randler et al., 2011].

1.3.2. Interspecific differences in manual laterality

The examples discussed in section 1.2.2 indicate that the manifestation of lateralised limb use varies considerably between different mammal species. Similarities and differences between species cannot be explained by their phylogenetic relatedness: closely related species may display contrasting laterality patterns, while representatives of phylogenetically distant taxa may show similar manual preferences [Scheumann et al., 2011; Meguerditchian et al., 2012; Ströckens et al., 2013]. Potential factors underlying the evolution of manual laterality in mammals were studied only in primates. The way of life and the gait are most often considered as the key characteristics of a species associated with the manifestation of manual laterality [MacNeilage, 1991; Ward, 1995; Meguerditchian et al., 2012].

Postural origins theory. This theory was first suggested in 1987 to explain differences in handedness between the species of primate [MacNeilage et al., 1987] and was later supplemented with new data. The postural origins theory of handedness proposes the mechanisms underlying the evolution of motor laterality in primates [MacNeilage, 1991, 2007]. According to this theory, population-level manual laterality first evolved in arboreal primates, which used the left hand mostly for capturing prey and the right hand for postural support. The left-hand preference for feeding can be explained by the right hemisphere dominance in the control of the spatial-temporal coordination of movements [MacNeilage, 1991]. In this way the right hand took up a complementary, accessory supporting function. The evolutionary change in the feeding niche and the transition to a terrestrial way of life resulted in changes in the distribution of roles between the primate hands. In mostly herbivorous terrestrial species the right hand, stronger because of its previous postural support role, in the course of evolution may have become favoured for processing food: nut-cracking, peeling fruit etc. [MacNeilage, 1991]. Postural origins theory of handedness has been supported with some recent data. Most of the arboreal primates studied in this respect use the left hand for feeding and the right hand for postural support [Ward, 1995; Milliken et al., 2005; Rigamonti et al., 2005]. In “high-level” (complex) tasks [Fagot, Vauclair, 1991] most arboreal primates demonstrate

a group-level left-hand preference, while most terrestrial primates demonstrate a right-hand preference [Morino, 2011; Meguerditchian et al., 2012].

Bipedalism theory. According to this theory, primates evolved a markedly expressed handedness in connection with bipedal locomotion. A comparative study of six species of Strepsirrhini showed that the more bipedal/vertical species were more strongly lateralised for feeding [Dodson et al., 1992, Ward et al., 1993]. These results suggest that bipedality/verticality may enhance motor lateralisation and that the gait was a key factor in the evolution of primate handedness [Ward, 1995]. It has also been proposed that bipedalism was responsible for the evolution of human handedness [Westergaard et al., 1998; Corbetta, 2003]: bipedal locomotion and the ensuing problem of balance control could result in a stronger lateralisation of the motor functions of the brain [Cashmore et al., 2008; Westergaard et al., 1998]. The results of studies dealing with the formation of handedness in human ontogenesis lend some support to this hypothesis. Until the age of three, human infants display unstable hand preferences, the change in the expression of handedness coinciding with the formation of new forms of locomotion [Corbetta, 2003]. Infants crawling on hands and feet (which is, in fact, a quadrupedal gait) show no stable patterns of hand preferences. These are established soon after an infant learns to walk, that is, adopts upright posture and bipedal gait.

1.4. Conclusion

The review of studies on lateralised limb use presented in this chapter, though far from complete, provides a retrospect of the evolution of views on this phenomenon in the last three decades. Gradually abandoning the idea of handedness as a strong lateralisation unique to humans, the researchers came to realise its relative nature (for instance, we know now that human handedness is weakly expressed for certain types of actions [Marchant et al., 1995]) and the existence of manual laterality in other animals (which may be as strong as human handedness [Ströckens et al., 2013; Giljov et al., 2015a]). The evolution of views on the nature of manual laterality was reflected in the modification of approaches to its study.

Limb laterality in animals is currently being studied in many different respects. The focus may be on developmental issues, on evolution, and adaptive significance of laterality or on nervous mechanisms underlying manual preferences. The widespread occurrence of lateralised limb use in various species [Ströckens et al., 2013] indicates that motor laterality is a fundamental feature of vertebrate animals.

That said, it should be noted that many animal groups remain poorly, if at all studied in respect of limb preferences. Primates have traditionally served as a model group for laterality studies [Hopkins, 2006], and primate research generated a number of hypotheses concerning the plasticity of manual laterality both within and between species. Whether these hypotheses are applicable to other mammals remains unclear because of the lack of information. Comprehensive studies of manual laterality in a different taxonomic group of mammals would provide an opportunity to test the universal nature of the generalisations made on primates.

Marsupials are a good candidate for the role of such model group. Being phylogenetically distant from primates, they also have numerous morphological and behavioural similarities with them [Schmitt, Lemelin, 2002; Weisbecker, Warton, 2006; Rassmussen, Sussman, 2007]. This means that they could serve as a convenient model for comparative laterality studies.

THE STUDY OF LATERALITY IN MARSUPIALS: SUBJECTS AND METHODS

2.1. Study sites and subjects

The subjects of this study were marsupial mammals (Mammalia: Marsupialia). Similarly to placentals (Mammalia: Placentalia), marsupials are a very diverse group. There are terrestrial, arboreal, subterranean, and semiaquatic species of marsupials [Garland et al., 1988; Karlen, Krubitzer, 2007]. There are among them herbivorous, predatory, and omnivorous species, highly social as well solitary species. Marsupials and placentals have evolved many similar adaptations to a certain way of life as a result of parallel evolution [Karlen, Krubitzer, 2007]. Parallelisms in morphological and behavioural specialisations are especially often found between marsupials and primates (Primates) [Schmitt, Lemelin, 2002; Weisbecker, Warton, 2006; Rassmussen, Sussman, 2007]. For instance, locomotor adaptations to terrestrial and arboreal way of life are very similar in these two groups [Garland et al., 1988; Schmitt, Lemelin, 2002; Weisbecker, Warton, 2006].

Marsupials possess very diverse locomotor characteristics. At the same time, all marsupial species can be generally divided into two groups: strictly quadrupedal species and species capable of both quadrupedal and bipedal locomotion [Windsor, Dagg, 1971; Kear et al., 2008]. It seems that bipedal hopping evolved in marsupials only once, within the Macropodoidea [Burk et al., 1998; Webster, Dawson, 2003]. This superfamily comprises three extant families: Hypsiprymnodontidae, Potoroidae and Macropodidae. The only extant representative of the family Hypsiprymnodontidae has no morphological adaptations to bipedalism and uses solely quadrupedal locomotion [Burk et al., 1998]. Bipedalism developed independently in two families, Potoroidae and Macropodidae, reaching its peak in species of the genus *Bettongia* (Potoroidae), large representatives of the genus *Macropus* (Macropodidae) and several extinct forms such as *Sthenurus* and *Procoptodon* (Macropodidae) [Webster, Dawson, 2003; Kear et al., 2008]. Many researchers consider the genus *Macropus*, including kangaroos and wallabies, to be paraphyletic. According to the modern classification, the genus *Macropus* is divided into three subgenera: *Notamacropus*, *Macropus*, and *Osphranter* [Meredith et al., 2009; Dawson, 2012].

2.1.1. Grey short-tailed opossum, *Monodelphis domestica* (Wagner, 1842)

Grey short-tailed opossums, *M. domestica* (Didelphimorphia, Didelphidae) are found in South America, where they inhabit forest, grassland and scrubland environments. They are solitary, nocturnal, mostly terrestrial animals [Eisenberg, Redford, 1999]. Grey short-tailed opossums mostly feed on insects, small rodents and fruit, and display nest-building behaviour [Fadem, Corbett, 1997]. Quadrupedal locomotion is characteristic of this species [Pridmore, 1992].

Data on grey short-tailed opossums (number of studied individuals $n = 26$: 12♂♂ and 14♀♀) were collected in the Scientific Research Department of the Moscow Zoo in March 2009 [Giljov et al., 2012a, 2013]. The age of the animals under study ranged from two to 39 months. The opossums were kept in cages 75×50×50 cm in size with an enriched environment (several shelters, branches etc.), one animal in a cage. The animals were exposed to artificial daylight switched on automatically for 15 h daily. Live insects (crickets *Gryllus* sp. and larvae of zophobas, *Zophobas morio*), finely chopped raw beef, boiled eggs and oatmeal porridge formed the basis of the opossums' diet. The opossums were daily provided with fresh nest material (hay and paper strips).

2.1.2. Sugar glider, *Petaurus breviceps* (Waterhouse, 1838)

Sugar gliders, *P. breviceps* (Diprotodontia, Petauridae) inhabit open forests of Australia, New Guinea and adjacent islands [Nowak, 1999]. They are nocturnal and shelter in nests situated in tree hollows during the daylight time. The basis of their diet is invertebrates and diverse plant food including sap and pollen [Smith, 1982]. Sugar gliders, a highly social species, live in groups of up to 12 individuals. They usually move quadrupedally but often rise on their hind limbs assuming a vertical posture, e.g., before a jump [Shapiro, Young, 2010].

Sugar gliders, *P. breviceps* ($n = 23$: 12♂♂ and 11♀♀), were observed in the Scientific Research Department of the Moscow Zoo in March 2009 [Giljov et al., 2013]. The studied individuals were aged from five to 66 months. Sugar gliders were kept in mixed-sex social groups in cages 77×37×130 cm in size with an enriched environment (several shelters, branches, ropes for climbing etc.). The animals were exposed to artificial daylight switched on automatically for 12 h daily. Their diet mostly consisted of various fruit cut into pieces and live insects (crickets *Gryllus* sp. and larvae of zophobas, *Zophobas morio*). The sugar gliders were daily provided with fresh nest material (hay and paper strips).

2.1.3. Goodfellow's tree kangaroo, *Dendrolagus goodfellowi* (Thomas, 1908)

The Goodfellow's tree kangaroo, *D. goodfellowi* (Diprotodontia, Macropodidae) is a species of tree kangaroos, which are adapted to life in tree tops [Flannery et al., 1996]. These animals occur in tropical rainforests of New Guinea. Goodfellow's tree kangaroo may be active both at night and in daylight. Similarly to other tree kangaroos, Goodfellow's tree kangaroos mostly feed on tree leaves and fruit, sometimes also eating flowers [Flannery et al., 1996].

Tree kangaroos evolved from terrestrial macropods (Macropodidae), most probably, from rock-wallabies of the genus *Petrogale*. However, in the course of evolution they have acquired a number of locomotor adaptations to an arboreal way of life [Martin, 2005]. For instance, in contrast to the other macropods, tree kangaroos are capable of alternating-limb locomotion and may move backwards [Flannery et al., 1996]. Tree kangaroos usually move quadrupedally on tree branches and bipedally — hopping or, rarely, walking — on the ground [Flannery et al., 1996; Martin, 2005]. In the wild these animals spend most of their lifetime on trees and rarely descend to the ground. Therefore, their usual gait is quadrupedal locomotion. Despite the ability of tree kangaroos to bipedal locomotion, the disproportion between the forelimbs and the hind limbs is weakly expressed in them as compared to other macropods [Kear et al., 2008]. Tree kangaroos show more freedom of forelimb movement than any other macropods [Martin, 2005], while their long claws, instead of inhibiting manual dexter-

ity, allow tree kangaroos to perform very fine manipulations of which other macropods are incapable [Iwaniuk et al., 1998].

Observations on Goodfellow's tree kangaroos, *D. goodfellowi* ($n = 14$), were made in three zoos in Germany: Krefeld Zoo (1♂ and 5♀), Dortmund Zoo (1♂ and 1♀) and Frankfurt Zoo (2♂♂ and 1♀) in September–October 2011, as well as in Taronga Zoo (Sydney, Australia) (1♂ and 2♀♀) in August 2013 [Giljov et al., 2012b, 2015a]. Goodfellow's tree kangaroos under study were aged from 10 months to 17 years. Most of the individuals were born in various zoos of Australia, the USA and Europe. The animals were kept either singly (Krefeld, Dortmund and Sydney Zoos) or in pairs (Frankfurt Zoo) in cages 200×100×300 cm in size connected to enclosures with an area of ca. 50 m². Cages were exposed to 12 h artificial daylight; the light in the enclosures was natural. The kangaroos were mostly fed on pieces of fruit, vegetables and fresh leafed branches.

2.1.4. Red-necked wallaby, *Macropus (Notamacropus) rufogriseus* (Desmarest, 1817)

Red-necked wallabies, locally known as Bennett's wallabies in Tasmania, *M. (N.) rufogriseus* (Diprotodontia, Macropodidae) inhabit forests and scrubland as well as various open landscapes of Australia and Tasmania [Frith, Calaby, 1969]. They are mostly crepuscular or nocturnal. Grasses, young shoots, and leaves of trees and shrubs form the basis of their diet. During periods of drought wallabies may also feed on plant roots. Red-necked wallabies live in small groups but may gather in larger groups during feeding [Frith, Calaby, 1969]. Bipedal hopping is their preferred gait at high and middle speed, while the quadrupedal position is characteristic of slow movement and during feeding on grass [Hume et al., 1989].

Data on **captive** red-necked wallabies, *M. (N.) rufogriseus* ($n = 27$) were collected in Leningrad Zoo (1♂), Moscow Zoo (7♂♂ and 2♀♀), Berlin Zoo (2♀♀), Kaliningrad Zoo (3♂♂ and 6♀♀) and Zoobotanico Jerez (2♂♂ and 4♀♀). Observations were conducted in spring and summer when wallabies are most active outside shelters: in Leningrad Zoo, in August 2008, in Moscow Zoo, in August 2009, in Berlin Zoo, in June 2010, in Kaliningrad Zoo, in July 2010 and in Zoobotanico Jerez, in March 2011. The exact age of the wallabies was unknown but all of them were mature (2 years and older). In Kaliningrad Zoo observations were also conducted on the red-necked wallaby young-at-foot aged 6–12 months, which continued to suckle but no longer re-entered the pouch; ($n = 6$). In Leningrad Zoo wallabies were kept singly in an enclosure with an area of 35 m². In Berlin, Moscow, Kaliningrad Zoos and Zoobotanico Jerez the wallabies were kept in mixed-sex groups in enclosures with an area of ca. 200, 100, 60 and 50 m², respectively. In all the zoos the enclosures had an adjoining shelter. Freshly mown grass and hay formed the basis of the wallabies' diet. They were also given fruits, vegetables, and grain.

Observations on **wild** red-necked wallabies were conducted during expeditions to Maria Island National Park (42°38'S 148°05' E, Tasmania, Australia) from 16 May to 16 June 2012 and from 17 October to 2 November 2013 [Giljov, Karenina, 2012; Giljov, 2014]. We collected both the data on adults ($n = 24$: 9♂♂ and 15♀♀) and on pouch young ($n = 11$). The numbers of red-necked wallabies on the island reach 5,000 individuals (ca. 460 individuals per km²) [Ingram, 2013]. Similarly to most other macropods (Macropodidae), red-necked wallabies are nocturnal and crepuscular [Hume et al., 1989], but on Tasmania and adjacent islands in the winter and spring of the Southern Hemisphere (that is, at the time of data collection) wallabies also regularly feed during daylight [Dawson, 2012].

2.1.5. Eastern grey kangaroo, *Macropus (Macropus) giganteus* (Shaw, 1790)

Eastern grey kangaroos, also known as Forester kangaroo in Tasmania *M. (M.) giganteus* (Diprotodontia, Macropodidae) inhabit various habitats from mountain forests and open woodland to coastal meadows, steppes, and semideserts of the mainland Australia and Tasmania [Frith, Calaby, 1969]. They are mainly crepuscular and nocturnal. Depending on the season and habitat, eastern grey kangaroos feed on various grasses, sometimes also on young shoots of shrubs and low shrubs [Dawson, 1995, 2012]. The largest social group of kangaroos is called a mob. It consists of individuals using the same territory during feeding [Dawson, 2012]. Within the mobs of eastern grey kangaroos there are stable groups of about six individuals (usually closely related), which move from place to place together. Young individuals and, sometimes, adult males may move from one mob to another [Dawson, 2012].

Locomotion of the eastern grey kangaroo is one of the most striking examples of bipedalism displayed by macropods and marsupials in general. Among modern macropods, only red kangaroos, *Macropus (Osphranter) rufus* have disproportionate bones of the hind limbs and other adaptations to bipedalism [Kear et al., 2008]. Eastern grey kangaroos usually move by bipedal hops. Quadrupedal gait (also referred to as pentapedal gait in large species of macropods because of the additional support on the tail) is used only during very slow locomotion [Seebeck, Rose, 1989; Webster, Dawson, 2003; Dawson, 2012].

Observations on **captive** eastern grey kangaroos, *M. (M.) giganteus* were conducted in Bonorong Wildlife Sanctuary (Tasmania, Australia) in June–July 2012 [Giljov, 2014]. We collected data both on adults ($n = 34$: 13♂♂ and 21♀♀) and on the young at two different stages of development: young-at-foot ($n = 12$); and pouch young ($n = 8$). A mixed-sex group (110–130 individuals) of eastern grey kangaroos was kept in an enclosed open-air territory with natural vegetation and an artificial pond. The kangaroos could find shelter in trees and shrubs in the retreat zone, occupying about a third of the enclosed area, where park visitors could not approach them. Since the kangaroos were fed during the day, they were mainly active during the daytime. Freshly mown grass and hay formed the basis of their diet; special pellets for macropods were given from time to time as a food supplement.

Wild eastern grey kangaroos ($n = 38$: 12♂♂ and 26♀♀) were observed during expeditions to Maria Island National Park (42°38' S 148°05' E, Tasmania, Australia) from 16 May to 16 June 2012 and from 17 October to 2 November 2013 [Giljov, 2014; Giljov et al., 2015a]. The numbers of the eastern grey kangaroo on the island reach about 2,000 individuals (ca. 180 individuals per km²) [Ingram, 2013]. Eastern grey kangaroos are crepuscular and nocturnal [Hume et al., 1989], but on Tasmania and adjacent islands in the winter and spring of the Southern Hemisphere (that is, at the time of data collection) they also regularly feed during daylight [Dawson, 2012].

2.1.6. Red kangaroo, *Macropus (Osphranter) rufus* (Desmarest, 1822)

Red kangaroos, *M. (O.) rufus* (Diprotodontia, Macropodidae) inhabit steppes, semideserts and deserts of Australia [Dawson, 2012]. They feed on grasses (*Eragrostis* sp.) and young shoots of shrubs, and low shrubs (mainly *Chenopodium*, *Atriplex* and *Maireana*) [Tyndale-Biscoe, 2005]. Mobs of red kangaroos consist of ca. 10–20 related individuals. This is one of the most territorial kangaroo species, dispersing almost exclusively at the expense of adult males and young individuals [Dawson, 2012]. The disproportion of hind limb bones and other

adaptations to bipedalism are especially strongly pronounced in this species as compared to other modern marsupials [Kear et al., 2008]. Bipedal hops are the preferred gait of red kangaroos; quadrupedal (pentapedal) gait is used only during very slow movement [Dawson, 2012].

Red kangaroos, *M. (O.) rufus* ($n = 41$: 15♂♂ and 26♀♀) were observed at Fowlers Gap Arid Zone Research Station of the University of New South Wales (31°21' S 141°39' E, New South Wales, Australia) from 14 August to 24 September 2013 [Giljov et al., 2015a]. The numbers of red kangaroos at Fowlers Gap, which has an area of ca. 40 ha, in winter and spring varies from 5,000 to 8,000 individuals depending on the air temperature and the amount of rainfall [Dawson, 2012].

2.1.7. Brush-tailed bettong, *Bettongia penicillata* (Grey, 1837)

Brush-tailed bettongs, also known as woylie, *B. penicillata* (Diprotodontia, Potoroidae) inhabit arid forested areas in Australia, avoiding grass and shrub thickets. These nocturnal animals feed on various parts of plants, mushrooms and invertebrates [Claridge et al., 2007]. This species builds nests made of grass, branches and tree bark. Brush-tailed bettongs are mostly solitary [Nowak, 1999].

Representatives of the family Potoroidae differ in the degree of bipedality. In contrast to species of *Potorous*, which usually move quadrupedally, species of *Bettongia* mainly move by bipedal hops. Brush-tailed bettongs, *B. penicillata* use quadrupedal locomotion very rarely, during very slow movement [Seebeck and Rose, 1989; Webster and Dawson, 2003].

Brush-tailed bettongs, *B. penicillata*, ($n = 15$) were observed in two zoos in Germany: in Berlin Zoo (5♂♂ and 5♀♀) in June 2010 and in Dortmund Zoo (2♂♂) in October 2011; observations were also conducted in the Scientific Research Department of the Moscow Zoo (2♂♂ and 1♀) in April 2012 [Giljov et al., 2012d]. In Berlin Zoo bettongs were kept in a mixed-sex group in a covered enclosure with glass walls, 400×250×250 cm in size. In Dortmund Zoo there were two bettongs kept together in a covered enclosure with glass walls, 400×350×250 cm in size. In the Scientific Research Department of the Moscow Zoo the bettongs were kept singly in cages with a size of ca. 300×100×200 cm. At all sites of data collection the bettongs' environment was enriched with artificial burrows, stones, branches etc. Daylight period was 12 h. Brush-tailed bettongs were mostly fed on nuts, fruit and vegetables cut into pieces as well as on live insects (locusts, *Locusta migratoria* and larvae of zophobas, *Zophobas morio*). Hay was used as nest material.

2.2. Collection of data on manual laterality in marsupials

2.2.1. Unimanual behaviours

At the early stages of studies on manual laterality, which are based on observations of animal behaviour, unimanual behaviours (actions in which the animals use only one forelimb) are identified [Boesch, 1991; Marchant, McGrew, 1996; Lonsdorf, Hopkins, 2005; Rigamonti et al., 2005; Zhao et al., 2008a; Lhota et al., 2009; Smith, Thompson, 2011]. In a preliminary study we identified the most frequent unimanual actions in all the species investigated in the present work except the Goodfellow's tree kangaroo, the eastern grey kangaroo and the red kangaroo. In these species laterality was studied for the same types of actions

as in the red-necked wallaby. The types of unimanual actions in marsupials were identified in the same way as in primate research [Boesch, 1991; Marchant, McGrew, 1996; Zhao et al., 2008a; Smith, Thompson, 2011]. We studied the similar behaviours in marsupials: manipulating food and non-food objects, use of a forelimb for supporting the body and use of a forelimb for grooming (self-cleaning) [Rigamonti et al., 2005; Hopkins, 2006]. Similarly to many studies conducted on primates [Hopkins, 1993; Westergaard et al., 1998; Blois-Heulin et al., 2007; Braccini et al., 2010], we registered separately the actions made by the marsupials from the quadrupedal position (when the animal was standing evenly on all four limbs before the beginning of the action) and from the bipedal position (before the beginning of the action the animal was standing on the two hind limbs with both forelimbs free and not touching the ground) (Figs. 1–3). Besides, we considered separately the use of limbs for feeding on non-living food and for catching live prey. The actions performed by animals in these two

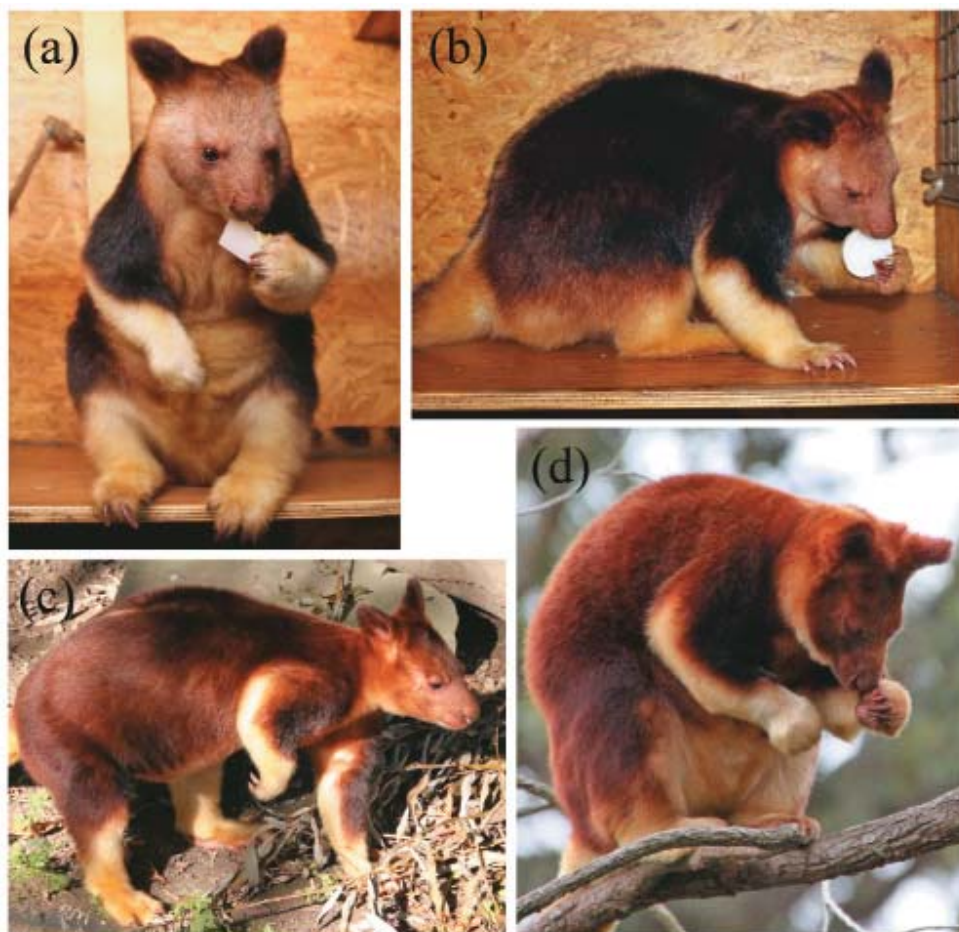


Fig. 1. Examples of unimanual behaviours in captive Goodfellow's tree kangaroos, *D. goodfellowi*. The use of one forelimb for feeding from the bipedal position (a), for feeding from the quadrupedal position (b), for supporting the body in the tripod stance (c) and for autogrooming (d).

types of situations are traditionally considered in primate research to have a different level of complexity [Fagot, Vauclair, 1991; King, Landau, 1993].

The use of one forelimb **for feeding** was registered as the use of a forelimb for taking a food object. Body posture (bipedal or quadrupedal) and food objects (hay, meat, fruit etc.) varied in the studied species of marsupials. **Use of one forelimb for catching live insects** was registered as the use of a forelimb for seizing an insect.

Tripedal stance is a posture of an animal standing on two hind limbs and a forelimb [Clark et al., 1993]. To analyse preferences for supporting the body in the tripedal stance, we registered the forelimb used by the animal as a prop. Grey short-tailed opossums and brush-tailed bettongs assuming the tripedal stance raised a forelimb from the initial quadrupedal position. On the contrary, Goodfellow's tree kangaroos, red-necked wallabies, eastern grey kangaroos and red kangaroos initially stood on two hind limbs and then put a forelimb on the ground.

When **supporting the body in the tripedal stance**, sugar gliders hanged upside down on a horizontal surface (the upper wall of the cage) gripping it with three limbs: two hind limbs and a forelimb. To assume this position, a sugar glider first hanged down using all the four limbs and then let go of one of the forelimbs. We registered the forelimb used to support the body, that is, the forelimb with which the sugar glider gripped the cage wall.

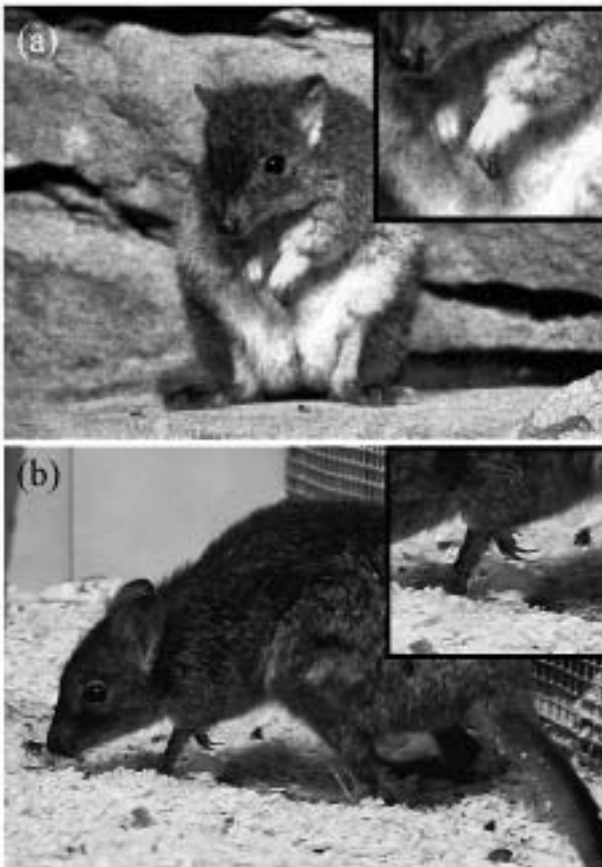


Fig. 2. Examples of unimanual behaviours in captive brush-tailed bettongs, *Bettongia penicillata*. The use of one forelimb for feeding on non-living food (a) and for supporting the body in the tripedal stance (b). Figure from Giljov et al., 2012d.



Fig. 3. Examples of unimanual behaviours in wild red-necked wallabies, *Macropus (Notamacropus) rufogriseus*. The use of one forelimb for feeding from the bipedal position (a), for feeding from the quadrupedal position (b), for supporting the body in the tripodal stance in adult individuals (c), as well as feeding on shrubs and trees with an asymmetrical participation of the forelimbs (d). Figure from Giljov et al., 2015a.

Manipulating nest material was registered when an animal pulled hay or a strip of paper towards itself with one forelimb. Unimanual actions aimed at cleaning the snout (the part of the body equidistant from both forelimbs) was registered as **autogrooming**.

In pouch young of red-necked wallaby and eastern grey kangaroo we registered the use of one forelimb for **manipulating food from the mother's pouch** (Fig. 4). Only the cases when both forelimbs were free before the manipulation were registered. We also registered the cases when the young **freed one forelimb from the pouch** (Fig. 4). In young-at-foot of red-necked wallaby and eastern grey kangaroo we registered the use of one forelimb for **pulling down the mother's pouch** during suckling (Fig. 4).

Unimanual behaviours differed in the seven species of marsupials under study. The types of actions examined for each of the species are described in more detail in Chapters 3 and 4.

To register unimanual behaviours, we video recorded the animals (usually several individuals at the same time) during the periods of maximum daily activity. Analysing the video

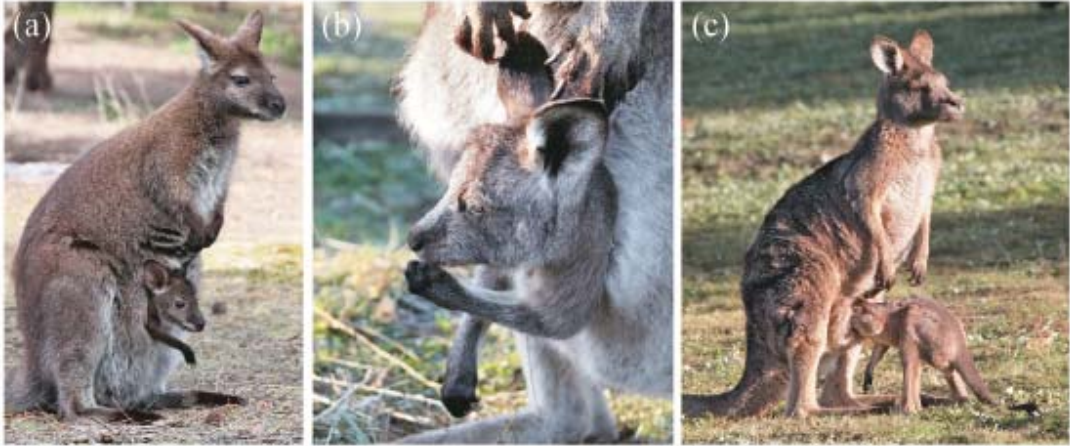


Fig. 4. Examples of unimanual behaviours in the young of marsupials. Freeing of one forelimb from the pouch in the young of red-necked wallaby, *M. (N.) rufogriseus* (a); the use of one forelimb for manipulating food from the mother's pouch (b) and for pulling down the mother's pouch during milk suckling (c) in eastern grey kangaroo, *M. (M.) giganteus*. Photos (b) and (c) from Giljov et al., 2017.

recordings, we scored the use of the left and the right forelimb separately from each individual and in each type of behaviour. A single use of the forelimb was considered as a single act. After an act has been registered, the next act was registered only after the animal moved to another place (made more than three steps quadrupedally). In this way, we obtained discrete acts of the use of a forelimb from each individual.

2.2.2. The study of captive animals

Material collected on each species studied in captivity included observations and video recordings of behaviour (Fig. 5) for 6–8 h a day during the peaks of the animals' activity [Giljov et al., 2012d, 2013]. The observer with a video camera was placed outside of the cage or enclosure. Grey short-tailed opossums and sugar gliders were observed in the hours of darkness for 14 days (in total, 104 h and 96 h of observations, respectively). Eastern grey kangaroos were observed during daylight hours for 15 days (in total, 118 h of observations). In different zoos the data were collected as follows: on the Goodfellow's tree kangaroo — during daylight hours for four to eight days (in total, 153 h of observations), on the red-necked wallaby — during daylight hours for 8–12 days (in total, 290 h of observations), on the brush-tailed bettong — during hours of darkness for 4–10 days (in total, 139 h of observations).

Video recordings were made with a Sony DCR-SR-220E digital video camera. Nocturnal species were filmed in the NightShot mode with infrared lighting. For individual identification of sugar gliders, small areas of fur were cut out at the back and/or the tail two days before the beginning of data collection. Animals of other species kept in groups were identified based on individual features of colouration and body shape.



Fig. 5. Observations and video recordings of behaviour of captive eastern grey kangaroos. The individual standing in the bipedal posture in the foreground in front of the observer raises food to the mouth with its left paw.

2.2.3. The study of wild animals

The data on wild marsupials was collected by observation and video recording of the behaviour. Data were collected for 32 days in 2012 and for 17 days in 2013 in case of the red-necked wallaby (in total, 192 h of observations) and the eastern grey kangaroo (in total, 239 h of observations) and for 42 days in 2013 (in total, 254 h of observations) in the case of the red kangaroo [Giljov, 2014; Giljov et al., 2015a]. Observations were conducted at the sites of the maximum concentration of the animals: for the red-necked wallaby, clearings in the woods and forest edges and for the eastern grey kangaroo, forest edges and coastal meadows. Red kangaroos were mostly observed in lowlands, in the areas with the greatest amount of young vegetation. Red-necked wallabies and eastern grey kangaroos were observed both during the day and at night. Red kangaroos were observed only during daylight hours.

Daytime observations. During the day animals were observed from a distance of ca. 30–60 m. We approached the animals using a recommended technique aimed at minimising disturbance to kangaroos [Wolf, Croft, 2010]. If an animal noticed our approach, we started to register the behaviour only after it stopped looking in the observer's direction. The animals were photographed in parallel with observations and video recordings. Video recordings were

made using a Sony DCR-SR-220E digital camera. Photos were made using a Canon EOS 500D camera and a Sigma AF18-250 mm F3.5-6.3 HSM camera lens.

A photo-catalogue of the studied individuals of each species was made in the course of the study. Individual identification was performed by comparing colouration and other individual features of the animals' appearance (mostly the features of head and ears) (Fig. 6). For each individual we registered the use of one forelimb for each behaviour, age class, sex and observation site.

Most of observations on red-necked wallabies and eastern grey kangaroos at Maria Island (Tasmania, Australia) were conducted throughout the daylight time (Fig. 7). Data collection was confined to the areas with the highest density of the animals, that is, treeless areas in the north of the island ("Darlington" area) and the central part of the island ("French's Farm" area). The closest borders of the two study areas were separated by a distance of 6 km. During the field season of 2012, the observations were conducted according to the following scheme: eight days in "Darlington" area — eight days in "French's Farm" area — eight days in "Darlington" area — eight days in "French's Farm" area. During the field season of 2013, the data were collected for seven days in "Darlington" area and for 10 days in "French's Farm" area.

The data on red kangaroos at Fowlers Gap Arid Zone Research Station (New South Wales, Australia) was collected in the morning and in the evening. Since hunting is forbidden at the station, the observer could come up much closer to the animals than in most other regions of Australia [Dawson, 2012].



Fig. 6. Photo-identification of an individual of the eastern grey kangaroo, *M. (M.) giganteus*. The match (photos of the same individual encountered twice) is framed. A photo-catalogue of the individuals made in the course of the study was used. Figure from Giljov et al., 2015a.

Night observations. During the field season of 2012, the data on eastern grey kangaroos and red-necked wallabies at Maria Island was collected also in the hours of darkness. An exact individual identification was therefore impossible but we could obtain data on more individuals than during the daytime. In this case, we used the route survey technique for behavioural observations and survey of macropods (Macropodidae) [Nielsen, 2009; Ingram, 2013]. Six routes were chosen in each study site (“Darlington” and “French’s Farm”). We searched for kangaroos and wallabies using red filter torches since they cause lesser disturbance to macropods than the usual ones [Nielsen, 2009]. After an animal was found, the red-filtered torch was switched off, and observations were conducted using a video camera in the NightShot mode and an infrared illuminator (Bars IK-K3) from a distance of 15–30 m (Fig. 8). This equipment made it possible to minimise the influence of the observer on the animal behaviour. Since 1994 night surveys of the abundance of macropods with the use of artificial lighting have been conducted at Maria Island three times a year. For this reason, red-necked wallabies and eastern grey kangaroos show a relatively low level of disturbance at the approach of the observer with a torch.

During the route survey, we registered one act of forelimb use in each type of behaviour from each encountered individual. As soon as one act in all types of behaviour was obtained from an individual, the observer began to collect data on the next animal. To survey as many individuals as possible, an animal was observed for not more than 10 minutes even if no use of one forelimb was registered. Observations on eastern grey



Fig. 7. Observations of red-necked wallabies at Maria Island (Tasmania, Australia).



Fig. 8. Night observations and registration of behaviour of wild animals: a — an eastern grey kangaroo in infrared light, b — a video camera in the NightShot mode equipped with an infrared illuminator (Bars IK-K3).

kangaroos and wallabies at each of the 12 survey routes were conducted twice, with an interval of eight days; the first time the data were collected in the beginning of the night (immediately after sunset) and the second time, in the end of the night (before sunrise). Since macropods constantly move within an individual area during the same activity period [Dawson, 2012], this scheme allowed us to minimise the probability of double records of the same individuals.

2.3. Statistical analysis

Statistical analysis of the data was performed using GraphPad Prism software package, ver. 6.03, 2013 (GraphPad Software, Inc., USA). Differences were considered significant at $p < 0.05$.

2.3.1. Assessment of individual manual preferences

To assess manual preferences in each individual, the frequency of use of the right and the left forelimb were compared separately in each unimanual behaviour. Individual preferences for each behaviour were assessed only in the individuals for which at least 15 acts of the use of one forelimb were obtained. In statistical analysis of the data on animals kept in the zoos, the same number of acts was used for all individuals within species for each behaviour; it was equal to the least number of acts obtained from an individual. In this way, we achieved standardisation of the number of analysed motor acts for all individuals in the studied sample in each behaviour. The standardisation was necessary because of the considerable scattering of the number of acts obtained from each individual. Since in the limited area of the cage (enclosure) all or at least several animals fall within the field of vision of a video camera and the activity periods are synchronised (for instance, because of the time of feeding), in the course of observations we continued to collect the data on individuals for which sufficient number of acts had already been obtained. When the data were collected in nature or under conditions close to natural ones (as in Bonorong Wildlife Sanctuary, Tasmania), we used for statistical analysis all the acts obtained

from an individual because of the considerable value of such data and a lesser scattering of the number of acts obtained from each individual as compared to observations of captive animals.

To identify individual preferences for each behaviour the number of acts of the use of the left forelimb and that of acts of the use of the right forelimb were compared using a binomial z test [Siegel, 1956]. Based on the results of the test, each individual was classified for each behaviour as lateralised, i.e. having a forelimb preference, or non-lateralised, i.e. having no forelimb preference. Lateralised individuals were identified as left-handers (individuals using the left forelimb significantly more often) or right-handers (individuals using the right forelimb significantly more often). To determine if the number of lateralised individuals differed from that of non-lateralised ones and if the number of left-handers differed from that of right-handers, the binomial z test was also used.

2.3.2. Assessment of group-level manual preferences

Preferences in the use of forelimbs at the level of the group were assessed using the handedness index [Strauss, Wada, 1983; Westergaard et al., 1998; Wells, 2003; Braccini et al., 2010; Hopkins et al., 2011; Meguerditchian et al., 2012]. Handedness index (HI) from each individual in each type of behaviour was calculated using the formula: $HI = (L-R)/(L+R)$, where L — number of acts of the left-forelimb use, and R—number of acts of the right-forelimb. HI values range from -1.0 to $+1.0$, with negative values indicating the right-forelimb bias, positive values indicating the left-forelimb bias, and values close to zero indicating the absence of preference

To check if the HI distribution for each behaviour was normal, a Shapiro-Wilk test was used [Shapiro, Wilk, 1965]. According to the test, the data were not normally distributed; therefore non-parametric tests were used for the analysis. Group-level laterality in the use of forelimbs in each species was assessed using one-sample Wilcoxon signed-rank test [Wilcoxon, 1945].

Analysing the data on wild red-necked wallabies and eastern grey kangaroos obtained by the route survey technique, we registered the first act of the forelimb use in each behaviour from each encountered individual. Laterality at the group level was assessed by comparing the number of acts of the use of the left and right forelimbs for each behaviour using a binomial z test [Siegel, 1956]. Comparison of motor preferences between the two areas of data collection was done with the use of a Z-test for proportions [Fleiss, 1981].

INDIVIDUAL AND GROUP-LEVEL MANUAL LATERALITY IN MARSUPIALS

Manual laterality may be expressed at the individual level and at the population level [Rogers, 2002]. Individual laterality is a statistically significant preference of an individual to use the left or the right limb. In general, individual manual preferences are stable though some variation is possible, and may be related, for instance, with ageing [Wells, Millsopp, 2012], disease [Zucca et al., 2011a], or stress [Rogers, 2009]. To assess population-level laterality, one should test the population for the predominance of left- or right-handers and to check whether there is a significant left- or right-hand bias in the mean values of laterality measures such as the handedness index [Westergaard et al., 1998; Rogers, 2002; Meguerditchian et al., 2012]. Many authors, especially those who study relatively small samples of captive animals, employ the term “group-level laterality” [Fagot, Vauclair, 1991].

3.1. Manual laterality in the grey short-tailed opossum, *Monodelphis domestica*

3.1.1. Unimanual behaviours

The use of one forelimb was studied in 26 grey short-tailed opossums kept in captivity in four behaviours: feeding on non-living food (sliced meat), catching live insects, supporting the body in the tripedal stance and manipulating nest material. Grey short-tailed opossums performed these unimanual actions from the quadrupedal position. They were very rarely observed in the bipedal posture. We obtained 45 acts of feeding on non-living food and 31 acts of capturing a live insect from each individual. We also obtained 40 acts of the use of one forelimb for supporting the body in the tripedal stance and 34 acts of the use of one forelimb for manipulating nest material from each individual.

3.1.2. Distribution of individual preferences and group-level laterality in the use of forelimbs

For feeding on non-living food, eight individuals (31%) demonstrated the left-forelimb preference, eight individuals (31%) demonstrated the right-forelimb preference and 10 individuals (38%) demonstrated no individual preference (Fig. 9; Table 1). The number of lateralised individuals did not differ from that of non-lateralised ones (binomial test, $z = 0.98$, $p = 0.327$). The number of left-handers was the same as that of right-handers.

Table 1.

Individual forelimb preferences during feeding in grey short-tailed opossum,
Monodelphis domestica in captivity

Subject, sex	Age, months	Feeding on non-living food						Catching of living insects					
		L	R	HI	<i>z</i>	<i>p</i>	Pref.	L	R	HI	<i>z</i>	<i>p</i>	Pref.
1♂	34	27	18	0.20	1.19	0.233	A	15	16	-0.03	0.00	1.000	A
2♂	21	10	35	-0.56	-3.72	<0.001	R	5	26	-0.68	-3.72	<0.001	R
3♂	2	23	22	0.02	0.00	1.000	A	8	23	-0.48	-2.55	0.011	R
4♂	14	31	14	0.38	2.41	0.016	L	23	8	0.48	2.55	0.011	L
5♂	17	11	34	-0.51	-3.35	<0.001	R	10	21	-0.35	-1.81	0.071	A
6♂	6	15	30	-0.33	-2.10	0.036	R	8	23	-0.48	-2.55	0.011	R
7♂	5	16	29	-0.29	-1.80	0.073	A	7	24	-0.55	-2.93	0.003	R
8♂	4	16	29	-0.29	-1.80	0.073	A	14	17	-0.10	-0.36	0.720	A
9♂	6	14	31	-0.38	-2.41	0.016	R	6	25	-0.61	-3.32	0.001	R
10♂	2	15	30	-0.33	-2.10	0.036	R	9	22	-0.42	-2.18	0.029	R
11♂	3	21	24	-0.07	-0.30	0.766	A	16	15	0.03	0.00	1.000	A
12♂	3	13	32	-0.42	-2.72	0.007	R	5	26	-0.68	-3.72	<0.001	R
13♀	6	26	19	0.16	0.89	0.371	A	11	20	-0.29	-1.44	0.150	A
14♀	21	29	16	0.29	1.80	0.073	A	19	12	0.23	1.08	0.281	A
15♀	21	25	20	0.11	0.60	0.552	A	17	14	0.10	0.36	0.720	A
16♀	17	14	31	-0.38	-2.41	0.016	R	25	6	0.61	3.32	<0.001	L
17♀	14	12	33	-0.47	-3.02	0.003	R	7	24	-0.55	-2.93	0.003	R
18♀	14	30	15	0.33	2.10	0.036	L	25	6	0.61	3.32	0.001	L
19♀	7	28	17	0.24	1.49	0.135	A	21	10	0.35	1.81	0.071	A
20♀	7	30	15	0.33	2.10	0.036	L	22	9	0.42	2.18	0.029	L
21♀	7	28	17	0.24	1.49	0.135	A	23	8	0.48	2.55	0.011	L
22♀	39	36	9	0.60	3.88	<0.001	L	27	4	0.74	3.95	<0.001	L
23♀	5	31	14	0.38	2.41	0.016	L	21	10	0.35	1.81	0.071	A
24♀	5	34	11	0.51	3.35	<0.001	L	22	9	0.42	2.18	0.029	L
25♀	2	32	13	0.42	2.72	0.007	L	22	9	0.42	2.18	0.029	L
26♀	2	34	11	0.51	3.35	<0.001	L	24	7	0.55	2.93	0.003	L

Here and later — L: the number of acts of left forelimb use. R: the number of acts of right forelimb use; HI: handedness index, positive values — left-sided bias, negative values — right-sided bias; *z*: binomial score. Pref.: individual preference in a forelimb use ($p < 0.05$), L — left forelimb preference, R — right forelimb preference, A — no preference.

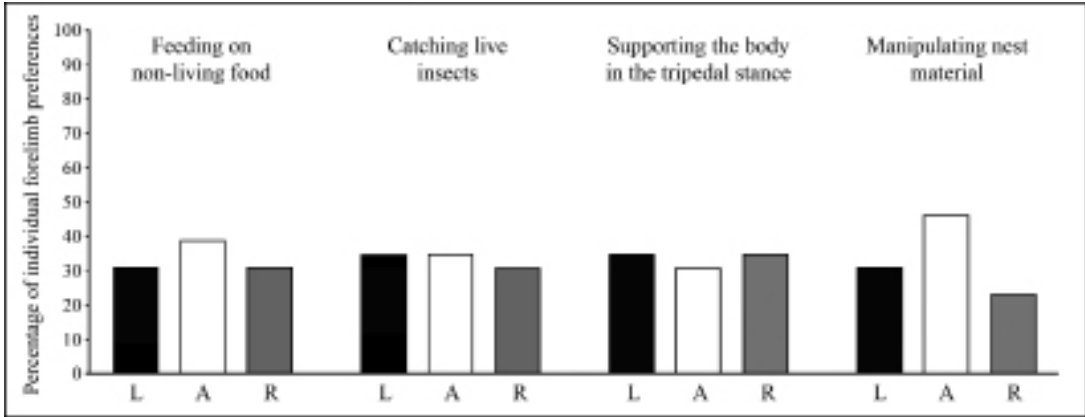


Fig. 9. Individual manual preferences in the grey short-tailed opossum [Giljov et al., 2012d, 2013]. Percentage of individuals demonstrating ($p < 0.05$): L — left-forelimb preference, R — right-forelimb preference; A — no preference.

For catching live insects, nine opossums (35%) showed the left-forelimb preference; eight opossums (30%) showed the right-forelimb preference; nine individuals (35%) showed no preference (Fig. 9; Table 1). No differences between the number of lateralised and that of non-lateralised individuals were found (binomial test, $z = 1.38$, $p = 0.169$). Neither did we find any differences between the number of left-handers and that of right-handers ($z = 0.00$, $p = 1.000$).

The left-forelimb preference for supporting the body in the tripodal stance was found in nine opossums (35%). The same number of individuals (35%) preferred to support the body using the right forelimb. Eight individuals (30%) demonstrated no preference (Fig. 9; Table 2). The number of lateralised individuals did not differ from that of non-lateralised ones (binomial test, $z = 1.78$, $p = 0.076$). The number of left-handers was the same as that of right-handers.

Eight grey short-tailed opossums (31%) showed the left-forelimb preference for manipulating nest material; six individuals (23%) showed the right-forelimb preference; 12 individuals (46%) showed no preference (Fig. 9; Table 2). We did not find any differences between the number of lateralised individuals and that of non-lateralised ones (binomial test, $z = 0.20$, $p = 0.845$). Neither did we find any differences between the number of left-handers and that of right-handers ($z = 0.27$, $p = 0.791$).

No group-level manual laterality was found in the grey short-tailed opossum (Fig. 10) for feeding on non-living food (mean HI \pm SEM = 0.03 ± 0.07 ; one-sample Wilcoxon signed-rank test, $W = 18$, $p = 0.827$, $n = 26$), catching live insects (mean HI = 0.02 ± 0.09 ; $W = 10$, $p = 0.905$, $n = 26$), supporting the body in the tripodal stance (mean HI = 0.02 ± 0.09 ; $W = -1$, $p = 0.995$, $n = 26$) and manipulating nest material (mean HI = 0.05 ± 0.09 ; $W = 40$, $p = 0.601$, $n = 26$).

Table 2.

Individual preferences in forelimb use for supporting of tripodal stance
and nest material collecting in grey short-tailed opossum,
Monodelphis domestica in captivity

Subject, sex	Age, months	Supporting of tripodal stance						Nest material collecting					
		L	R	HI	z	p	Pref.	L	R	HI	z	p	Pref.
1♂	34	17	23	-0.15	-0.18	0.430	A	5	29	-0.71	-3.94	<0.001	R
2♂	21	7	33	-0.65	-3.95	<0.001	R	6	28	-0.65	-3.72	<0.001	R
3♂	2	24	16	0.20	1.11	0.268	A	21	13	0.24	1.20	0.230	A
4♂	14	27	13	0.35	2.07	0.039	L	28	6	0.65	3.72	0.000	L
5♂	17	11	29	-0.45	-2.73	0.006	R	8	26	-0.53	-2.98	0.003	R
6♂	6	9	31	-0.55	-3.39	0.001	R	12	22	-0.29	-1.55	0.121	A
7♂	5	8	32	-0.60	-3.72	0.000	R	11	23	-0.35	-1.90	0.058	A
8♂	4	14	26	-0.30	-1.75	0.081	A	19	15	0.12	0.51	0.608	A
9♂	6	11	29	-0.45	-2.73	0.006	R	10	24	-0.41	-2.25	0.024	R
10♂	2	12	28	-0.40	-2.40	0.017	R	21	13	0.24	1.20	0.230	A
11♂	3	12	28	-0.40	-2.40	0.017	R	15	19	-0.12	-0.51	0.608	A
12♂	3	10	30	-0.50	-3.06	0.002	R	4	30	-0.76	-4.29	<0.001	R
13♀	6	9	31	-0.55	-3.39	<0.001	R	17	17	0.00	0.00	1.000	A
14♀	21	22	18	0.10	0.47	0.636	A	15	19	-0.12	-0.51	0.608	A
15♀	21	28	12	0.40	2.40	0.017	L	27	7	0.59	3.16	0.001	L
16♀	17	34	6	0.70	4.27	<0.001	L	22	12	0.29	1.55	0.121	A
17♀	14	21	19	0.05	0.16	0.875	A	13	21	-0.24	-1.20	0.230	A
18♀	14	27	13	0.35	2.07	0.039	L	25	9	0.47	2.61	0.009	L
19♀	7	25	15	0.25	1.43	0.154	A	18	16	0.06	0.17	0.864	A
20♀	7	30	10	0.50	3.06	0.002	L	24	10	0.41	2.25	0.024	L
21♀	7	24	16	0.20	1.11	0.268	A	9	25	-0.47	-2.61	0.009	R
22♀	39	32	8	0.60	3.72	<0.001	L	25	9	0.47	2.61	0.009	L
23♀	5	27	13	0.35	2.07	0.039	L	23	11	0.35	1.90	0.058	A
24♀	5	29	11	0.45	2.73	0.006	L	31	3	0.82	4.63	<0.001	L
25♀	2	26	14	0.30	1.75	0.081	A	27	7	0.59	3.16	<0.001	L
26♀	2	32	8	0.60	3.72	<0.001	L	29	5	0.71	3.94	<0.001	L

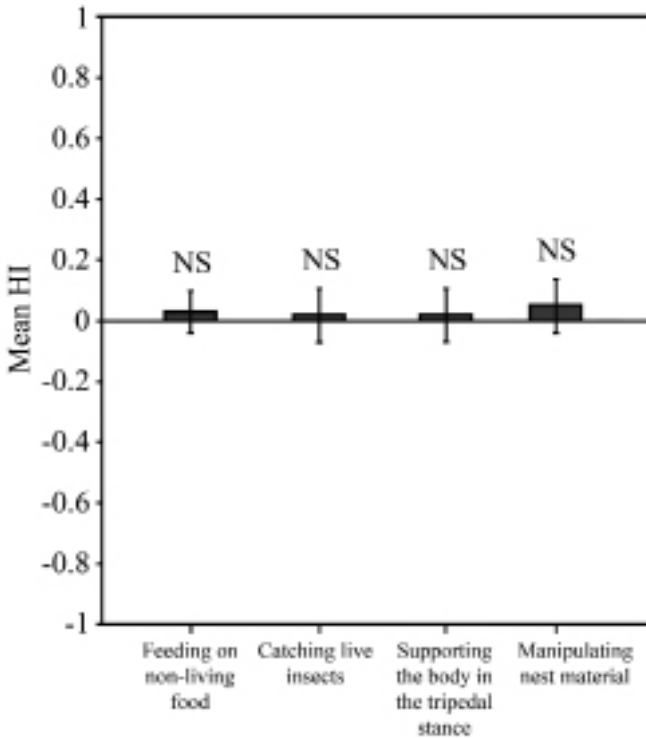


Fig. 10. The absence of group-level manual laterality in the grey short-tailed opossum. HI — handedness index: positive values — left-forelimb bias; negative values — right-forelimb bias; NS — not significant.

3.2. Manual laterality in the sugar glider, *Petaurus breviceps*

3.2.1. Unimanual behaviours

Manual preferences were studied in 23 captive sugar gliders for feeding on non-living food (cut fruits), catching live insects and supporting the body in the tripodal stance. In 19 individuals manual preferences for manipulating nest material were also studied. Sugar gliders performed all these actions from the quadrupedal position. From time to time, however, they assumed the bipedal position, manipulating objects with both paws or examining something situated above them.

We obtained 28 acts of the use of one forelimb during feeding on non-living food from each sugar glider. To identify manual preferences for catching live insects, 36 acts of seizing an insect were obtained from each individual. Supporting the body in the tripodal stance, the sugar gliders hanged on a horizontal surface (the roof of the cage) using three limbs: two hind limbs and a forelimb. From each individual, 47 acts of using one forelimb for supporting the body in the tripodal stance during hanging were obtained. For manipulating nest material, 25 acts of the use of one forelimb were obtained from each individual.

3.2.2. Distribution of individual and group-level manual preferences

For feeding on non-living food, 11 individuals of sugar gliders (48%) showed the left-forelimb preference, five individuals (22%) showed the right-forelimb preference, and seven individuals (30%) showed no preference (Fig. 11; Table 3). The number of lateralised individuals did not differ significantly from that of non-lateralised ones (binomial test, $z = 1.67$, $p = 0.093$). The number of left-handers did not differ from that of right-handers ($z = 1.25$, $p = 0.210$).

Table 3.

Individual preferences in forelimb use for feeding in sugar glider,
Petaurus breviceps in captivity

Subject, sex	Age, months	Feeding on non-living food						Catching of living insects					
		L	R	HI	z	p	Pref.	L	R	HI	z	p	Pref.
1♂	42	7	21	-0.50	-2.50	0.013	R	14	22	-0.22	-1.17	0.243	A
2♂	25	11	17	-0.21	-0.94	0.345	A	15	21	-0.17	-0.83	0.405	A
3♂	27	9	19	-0.36	-1.71	0.087	A	20	16	0.11	0.50	0.618	A
4♂	15	4	24	-0.71	-3.54	0.000	R	9	27	-0.50	-2.89	0.004	R
5♂	16	20	8	0.43	1.80	0.036	L	25	11	0.39	2.19	0.029	L
6♂	13	12	16	-0.14	-0.57	0.572	A	14	22	-0.22	-1.17	0.243	A
7♂	13	23	5	0.64	3.32	0.001	L	27	9	0.50	2.89	0.004	L
8♂	12	7	21	-0.50	-2.24	0.013	R	10	26	-0.44	-2.28	0.011	R
9♂	6	6	22	-0.57	-2.90	0.004	R	2	34	-0.89	-5.17	<0.001	R
10♂	10	16	12	0.14	0.57	0.572	A	13	23	-0.28	-1.50	0.133	A
11♂	15	25	3	0.79	3.97	<0.001	L	28	8	0.56	3.24	0.001	L
12♂	6	17	11	0.21	0.94	0.345	A	20	16	0.11	0.50	0.618	A
13♀	48	24	4	0.71	3.54	0.000	L	30	6	0.67	3.83	<0.001	L
14♀	46	20	8	0.43	1.80	0.036	L	25	11	0.39	2.19	0.029	L
15♀	45	13	15	-0.07	-0.19	0.851	A	15	21	-0.17	-0.83	0.405	A
16♀	25	2	26	-0.86	-4.35	<0.001	R	9	27	-0.50	-2.89	0.004	R
17♀	26	17	11	0.21	0.94	0.345	A	28	8	0.56	3.24	0.001	L
18♀	24	21	7	0.50	2.50	0.013	L	29	7	0.61	3.62	0.000	L
19♀	17	25	3	0.79	3.97	<0.001	L	31	5	0.72	4.17	<0.001	L
20♀	13	23	5	0.64	3.32	<0.001	L	29	7	0.61	3.62	<0.001	L
21♀	8	25	3	0.79	3.97	<0.001	L	16	20	-0.11	-0.50	0.618	A
22♀	10	20	8	0.43	1.80	0.036	L	22	14	0.22	1.17	0.243	A
23♀	12	22	6	0.57	2.90	0.004	L	26	10	0.44	2.28	0.011	L

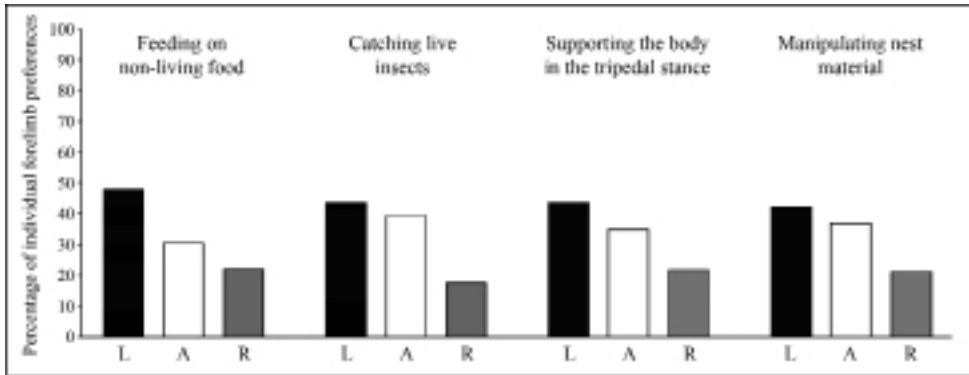


Fig. 11. Individual manual preferences in the sugar glider [Giljov et al., 2013]. Designations as in Fig. 9.

For catching live insects, 10 sugar gliders (44%) preferred to use the left forelimb; four individuals (17%) preferred to use the right forelimb; nine individuals (39%) showed no preference (Fig. 11; Table 3). No significant differences between the number of lateralised individuals and that of non-lateralised ones were found (binomial test, $z = 0.83, p = 0.845$). The number of left-handers and that of right-handers did not differ significantly, either ($z = 1.34, p = 0.180$).

The preference to support the body in the tripedal stance with the left forelimb was found in 10 individuals (43%), five (22%) preferred to use the right forelimb and eight sugar gliders

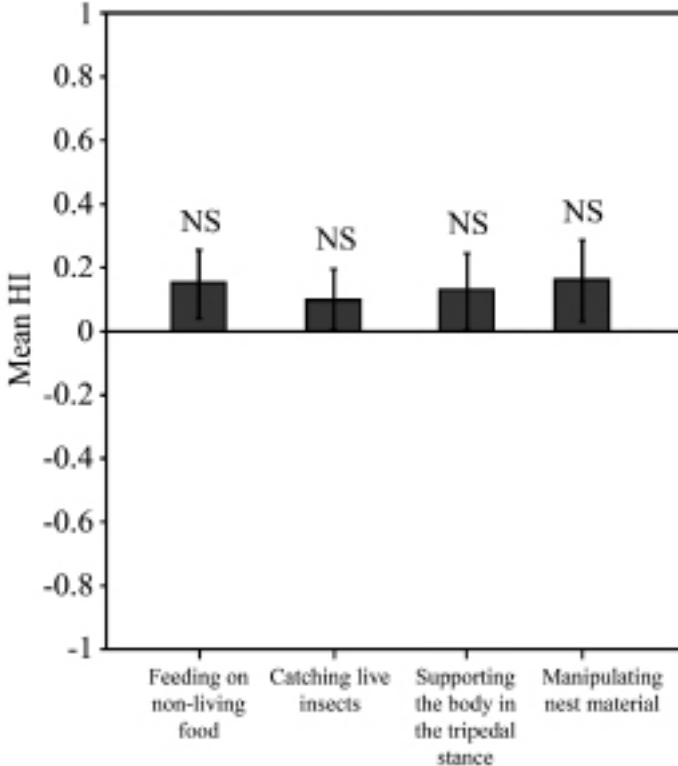


Fig. 12. Absence of group-level manual laterality in the sugar glider. Designations as in Fig. 10.

(35%) showed no preference (Fig. 11; Table 4). The number of lateralised individuals did not differ significantly from that of non-lateralised ones (binomial test, $z = 1.25$, $p = 0.210$). The number of left-handers did not differ from that of right-handers ($z = 1.03$, $p = 0.302$).

Left-forelimb preference for manipulating nest material was found in eight individuals (42%), right-forelimb preference was found in four individuals (21%), seven sugar gliders (37%) showed no preference (Fig. 11; Table 4). No significant differences between the number of lateralised individuals and that of non-lateralised ones were found (binomial test, $z = 0.92$, $p = 0.359$). No significant differences between the number of left-handers and that of right-handers were found, either ($z = 0.87$, $p = 0.388$).

No group-level manual laterality was found in the sugar gliders (Fig. 12) for feeding on non-living food (mean HI \pm SEM = 0.15 ± 0.11 ; one-sample Wilcoxon signed-rank test, $W = 85$, $p = 0.202$, $n = 23$), for catching live insects (mean HI = 0.10 ± 0.10 ; $W = 77$, $p = 0.249$, $n = 23$), for supporting the body in the tripod stance (mean HI = 0.13 ± 0.12 ; $W = 75$, $p = 0.263$, $n = 23$) or for manipulating nest material (mean HI = 0.16 ± 0.13 ; $W = 61$, $p = 0.229$, $n = 19$).

Table 4.

Individual preferences in forelimb use for supporting of tripod stance and nest material collecting in sugar glider, *Petaurus breviceps* in captivity

Subject, sex	Age, months	Supporting of tripod stance						Nest material collecting					
		L	R	HI	z	p	Pref.	L	R	HI	z	p	Pref.
1♂	42	12	35	-0.49	-3.26	0.001	R	8	17	-0.36	-1.61	0.108	A
2♂	25	9	38	-0.62	-4.08	<0.001	R	5	20	-0.60	-2.87	0.004	R
3♂	27	20	27	-0.15	-0.87	0.382	A	10	15	-0.20	-0.8	0.424	A
4♂	15	18	29	-0.23	-1.46	0.144	A	–	–	–	–	–	–
5♂	16	42	5	0.79	5.25	<0.001	L	22	3	0.76	3.6	<0.001	L
6♂	13	22	25	-0.06	-0.29	0.771	A	6	19	-0.52	-2.44	0.015	R
7♂	13	30	17	0.28	1.76	0.079	A	14	11	0.12	0.4	0.690	A
8♂	12	8	39	-0.66	-4.38	<0.001	R	–	–	–	–	–	–
9♂	6	3	44	-0.87	-5.83	<0.001	R	7	18	-0.44	-2.02	0.043	R
10♂	10	18	29	-0.23	-1.46	0.144	A	9	16	-0.28	-1.2	0.230	A
11♂	15	33	14	0.40	2.66	0.008	L	–	–	–	–	–	–
12♂	6	37	10	0.57	3.79	<0.001	L	13	12	0.04	0	1.000	A
13♀	48	44	3	0.87	5.83	<0.001	L	23	2	0.84	4	<0.001	L
14♀	46	22	25	-0.06	-0.29	0.771	A	20	5	0.60	2.87	0.004	L
15♀	45	20	27	-0.15	-0.87	0.382	A	4	21	-0.68	-3.32	<0.001	R
16♀	25	6	41	-0.74	-4.96	<0.001	R	9	16	-0.28	-1.2	0.230	A
17♀	26	47	0	1.00	6.71	<0.001	L	22	3	0.76	3.6	<0.001	L
18♀	24	34	13	0.45	2.96	0.003	L	19	6	0.52	2.44	0.015	L
19♀	17	39	8	0.66	4.38	<0.001	L	24	1	0.92	4.4	<0.001	L
20♀	13	41	6	0.74	4.96	<0.001	L	21	4	0.68	3.32	<0.001	L
21♀	8	30	17	0.28	1.76	0.079	A	14	11	0.12	0.4	0.690	A
22♀	10	33	14	0.40	2.66	0.008	L	–	–	–	–	–	–
23♀	12	45	2	0.91	6.13	<0.001	L	25	0	1.00	4.8	<0.001	L

3.3. Manual laterality in the Goodfellow's tree kangaroo, *Dendrolagus goodfellowi*

3.3.1. Unimanual behaviours

The use of one forelimb was studied in 14 captive Goodfellow's tree kangaroos in four behaviours: feeding from the quadrupedal position, feeding from the bipedal position, supporting the body in the tripedal stance and autogrooming (Fig. 1) [Giljov et al., 2015a]. For the analysis of manual preferences for feeding, we obtained from each individual 46 acts of the use of one limb for taking food (sliced fruit and vegetables) from the bipedal position and 72 acts of the use of one limb for taking food from the quadrupedal position. For the analysis of the use of one forelimb for supporting the body in the tripedal stance, 39 acts were obtained from each individual. To assess manual preferences for autogrooming, we registered unimanual snout autogrooming acts, which kangaroos perform from the bipedal position. The use of one forelimb was registered only if both forelimbs were free and above the ground surface before the start of autogrooming and if the kangaroo was not using them for any actions. We obtained 25 acts of the use of one limb for autogrooming from each individual.

3.3.2. Distribution of individual and group-level manual preferences

The same distribution of individual preferences was found in two behaviours of Goodfellow's tree kangaroos: feeding from the bipedal position and feeding from the quadrupedal position. The left-forelimb preference was observed in four individuals (29%); the right-forelimb preference was observed in six individuals (42%); in four kangaroos (29%) no preference was found (Fig. 13; Table 5). The number of lateralised individuals did not differ significantly from that of non-lateralised ones (binomial test, $z = 1.34$, $p = 0.180$). No significant differences between the number of left-handers and that of right-handers were found, either ($z = -0.32$, $p = 0.754$).

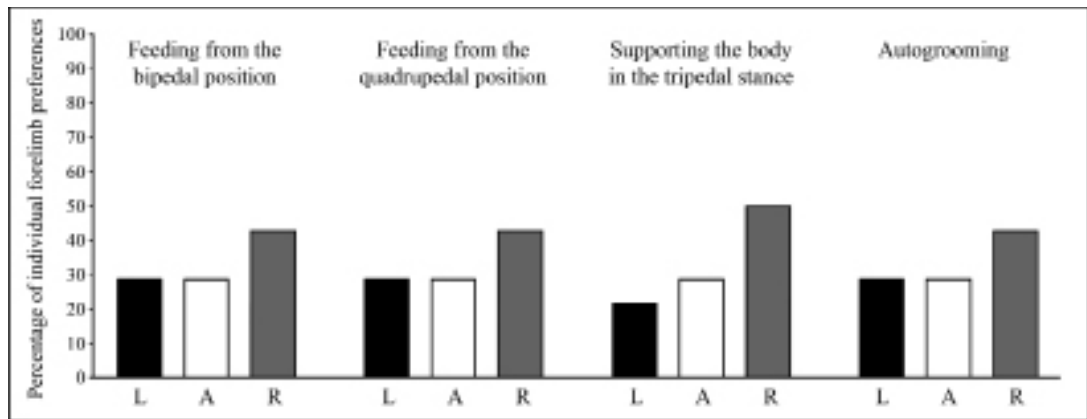


Fig. 13. Individual manual preferences in the Goodfellow's tree kangaroo. Designations as in Fig. 9.

Table 5.

Individual preferences in forelimb use for supporting of tripedal stance and nest material collecting in sugar glider, *Petaurus breviceps* in captivity

Subject, sex	Age, months	Feeding from the bipedal position						Feeding from the quadrupedal position					
		L	R	HI	z	p	Pref.	L	R	HI	z	p	Pref.
1♂	95	3	43	-0.87	-5.75	<0.001	R	5	67	-0.86	-7.19	<0.001	R
2♂	151	2	44	-0.91	-6.05	<0.001	R	2	70	-0.94	-7.90	<0.001	R
3♂	201	5	41	-0.78	-5.16	<0.001	R	4	68	-0.89	-7.42	<0.001	R
4♂	98	24	22	0.04	0.15	0.883	A	39	33	0.08	0.59	0.556	A
5♂	39	34	12	0.48	3.10	0.002	L	54	18	0.50	4.12	<0.001	L
6♀	175	25	21	0.09	0.44	0.659	A	37	35	0.03	0.12	0.906	A
7♀	110	32	14	0.39	0.15	0.883	L	61	11	0.69	5.77	<0.001	L
8♀	111	17	29	-0.26	-1.62	0.104	A	31	41	-0.14	-1.06	0.289	A
9♀	10	3	43	-0.87	-5.75	<0.001	R	1	71	-0.97	-8.13	<0.001	R
10♀	76	3	43	-0.87	-5.75	<0.001	R	9	63	-0.75	-6.25	<0.001	R
11♀	132	16	30	-0.30	-1.92	0.054	A	34	38	-0.06	-0.35	0.724	A
12♀	23	41	5	0.78	5.16	<0.001	L	62	10	0.72	6.01	<0.001	L
13♀	205	45	1	0.96	5.66	<0.001	L	69	3	0.92	7.66	<0.001	L
14♀	81	2	44	-0.91	-5.58	<0.001	R	16	56	-0.56	-4.60	<0.001	R

Table 6.

Individual preferences in forelimb use for supporting of tripedal stance and autogrooming in Goodfellow's tree-kangaroo, *Dendrolagus goodfellowi* in captivity

Subject, sex	Age, months	Supporting of tripedal stance						Autogrooming					
		L	R	HI	z	p	Pref.	L	R	HI	z	p	Pref.
1♂	95	8	31	-0.59	-3.52	<0.001	R	9	16	-0.28	-1.20	0.230	A
2♂	151	33	6	0.69	4.16	<0.001	L	1	24	-0.92	-4.40	<0.001	R
3♂	201	10	29	-0.49	-2.88	0.003	R	3	22	-0.76	-3.60	<0.001	R
4♂	98	3	36	-0.85	-5.12	<0.001	R	2	23	-0.84	-4.00	<0.001	R
5♂	39	32	7	0.64	3.84	<0.001	L	20	5	0.60	2.80	0.004	L
6♀	175	14	25	-0.28	-1.60	0.108	A	11	14	-0.12	-0.40	0.690	A
7♀	110	31	8	0.59	3.52	<0.001	L	22	3	0.76	3.60	<0.001	L
8♀	111	22	17	0.13	0.64	0.522	A	17	8	0.36	1.60	0.108	A
9♀	10	19	20	-0.03	0.00	1.000	A	0	25	-1.00	-4.80	<0.001	R
10♀	76	0	39	-1.00	-6.08	<0.001	R	6	19	-0.52	-2.40	0.015	R
11♀	132	19	20	-0.03	0.00	1.000	A	13	12	0.04	0.00	1.000	A
12♀	23	5	34	-0.74	-4.48	<0.001	R	19	6	0.52	2.40	0.015	L
13♀	205	7	32	-0.64	-3.84	<0.001	R	24	1	0.92	4.40	<0.001	L
14♀	81	3	36	-0.85	-5.12	<0.001	R	4	21	-0.68	-3.20	0.001	R

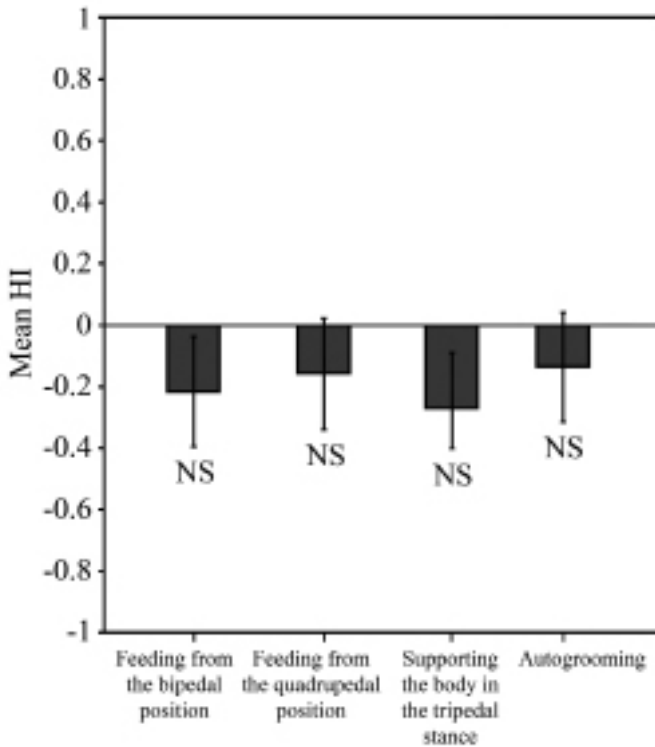


Fig. 14. The absence of group-level laterality in the Goodfellow's tree kangaroo. Designations as in Fig. 10.

Three Goodfellow's tree kangaroo (21%) preferred to support the body in the tripodal stance using the left forelimb; seven individuals (50%) preferred to use the right forelimb; in four individuals (29%) no statistically significant preference was found (Fig. 13; Table 6). The number of lateralised individuals did not differ significantly from that of non-lateralised ones (binomial test, $z = 1.34$, $p = 0.180$). The number of left-handers did not differ from that of right-handers ($z = -0.95$, $p = 0.344$).

Left-forelimb preference for autogrooming was found in four kangaroos (29%); right-forelimb preference was found in six individuals (42%); four individuals (29%) showed no preference (Fig. 13; Table 6). No significant differences between the number of lateralised individuals and that of non-lateralised ones were found (binomial test, $z = 1.34$, $p = 0.180$). The number of right-handers did not differ significantly from that of left-handers ($z = -0.32$, $p = 0.754$).

No group-level preference of the left forelimb for any of the studied behaviours was found in Goodfellow's tree kangaroo (Fig. 14) (feeding from the bipedal position: mean HI \pm SEM = -0.22 ± 0.18 , one-sample Wilcoxon signed-rank test, $W = -35$, $p = 0.288$, $n = 14$; feeding from the quadrupedal position: mean HI = -0.16 ± 0.18 , $W = -33$, $p = 0.326$, $n = 14$; supporting the body in the tripodal stance: mean HI = -0.25 ± 0.16 , $W = -49$, $p = 0.131$, $n = 14$; autogrooming: mean HI = -0.14 ± 0.18 ; $W = -26$, $p = 0.434$, $n = 14$).

3.4. Manual laterality in the red-necked wallaby, *Macropus (Notamacropus) rufogriseus*

3.4.1. Laterality in captive individuals

3.4.1.1. Unimanual behaviours

Adults. The use of one forelimb was studied in 27 adult red-necked wallabies for feeding from the bipedal position, feeding from the quadrupedal position and for supporting the body in the tripodal stance [Giljov et al., 2012c]. In nine individuals manual preferences for autogrooming were also studied [Giljov et al., 2012c]. From each individual we obtained 24 acts of unimanual food reaching from the bipedal position and 24 acts of that from the quadrupedal position. We also obtained 53 acts of supporting the body in the tripodal stance from each individual. For autogrooming, 10 acts of the use of one forelimb for snout autogrooming from the bipedal position were obtained from each individual.

Young. Six red-necked wallaby young-at-foot were studied. To reach the teat, young wallabies put their head into the mother's pouch, simultaneously pulling down the edge of the pouch with both forelimbs. Having put its head into the pouch and having started suckling, the young wallaby usually put one of the forelimbs on the ground, continuing to pull down the edge of the pouch with the other forelimb for the entire duration of the suckling (Fig. 4c). Young red-necked wallabies usually suckled furtively, mostly in the dark, and therefore this behaviour was rarely observed. We registered each case of asymmetric limb use for suckling but managed to obtain at least 10 acts of the use of one forelimb only from two young wallabies out of the six studied.

3.4.1.2. Distribution of individual preferences and group-level laterality in the use of forelimbs

Adults. For feeding from the bipedal position, 20 individuals (74%) preferred to use the left forelimb, two individuals (7%) preferred to use the right forelimb, and five individuals (19%) showed no preference (Fig. 15; Table 7). Most individuals were lateralised (binomial test, $z = 3.08$, $p = 0.002$), with most of the lateralised individuals being left-handed ($z = 3.62$, $p < 0.001$).

The analysis of the data on feeding from the quadrupedal position showed that 24 wallabies (89%) had no statistically significant preference and three individuals (11%) preferred to use the left forelimb (Fig. 15; Table 7). Most of the studied individuals were non-lateralised for this behaviour (binomial test, $z = -3.85$, $p < 0.001$).

For supporting the body in the tripodal stance, the left-forelimb preference was found in three individuals (11%), the right-forelimb preference was found in 14 individuals (52%), and no preference was found in 10 wallabies (37%) (Fig. 15; Table 8). The number of lateralised individuals did not differ from that of non-lateralised ones (binomial test, $z = 1.15$, $p = 0.248$), but most lateralised wallabies preferred to support the body with the right forelimb ($z = 2.43$, $p = 0.013$). For autogrooming, five individuals (56%) preferred to use the left forelimb, while four individuals (44%) showed no preference (Table 8).

Table 7.

Individual preferences in forelimb use for feeding in adult red-necked wallaby,
Macropus (Notamacropus) rufogriseus in captivity

Subject, sex	Feeding from the bipedal position						Feeding from the quadrupedal position					
	L	R	HI	<i>z</i>	<i>p</i>	Pref.	L	R	HI	<i>z</i>	<i>p</i>	Pref.
1♂	18	6	0.50	2.45	0.014	L	14	10	0.17	0.82	0.414	A
2♂	20	4	0.67	3.27	0.001	L	12	12	0.00	0.00	1.000	A
3♂	21	3	0.75	3.67	0.000	L	10	14	-0.17	-0.82	0.414	A
4♂	17	7	0.42	2.04	0.041	L	13	11	0.08	0.41	0.683	A
5♂	20	4	0.67	3.27	0.001	L	14	10	0.17	0.82	0.414	A
6♂	5	19	-0.58	-2.86	0.004	R	9	15	-0.25	-1.22	0.221	A
7♂	23	1	0.92	4.49	<0.001	L	18	6	0.50	2.45	0.014	L
8♂	19	5	0.58	2.86	0.004	L	11	13	-0.08	-0.41	0.683	A
9♂	17	7	0.42	2.04	0.041	L	14	10	0.17	0.82	0.414	A
10♂	14	10	0.17	0.82	0.414	A	13	11	0.08	0.41	0.683	A
11♂	18	6	0.50	2.45	0.014	L	15	9	0.25	1.22	0.221	A
12♂	22	2	0.83	4.08	<0.001	L	10	14	-0.17	-0.82	0.414	A
13♂	18	6	0.50	2.45	0.014	L	17	7	0.42	2.04	0.041	L
14♀	15	9	0.25	1.22	0.221	A	13	11	0.08	0.41	0.683	A
15♀	21	3	0.75	3.67	<0.001	L	16	8	0.33	1.63	0.102	A
16♀	16	8	0.33	1.63	0.102	A	12	12	0.00	0.00	1.000	A
17♀	6	18	-0.50	-2.45	0.014	R	10	14	-0.17	-0.82	0.414	A
18♀	12	12	0.00	0.00	1.000	A	11	13	-0.08	-0.41	0.683	A
19♀	21	3	0.75	3.67	<0.001	L	14	10	0.17	0.82	0.414	A
20♀	19	5	0.58	2.86	0.004	L	12	12	0.00	0.00	1.000	A
21♀	17	7	0.42	2.04	0.041	L	14	10	0.17	0.82	0.414	A
22♀	11	13	-0.08	-0.41	0.683	A	9	15	-0.25	-1.22	0.221	A
23♀	20	4	0.67	3.27	0.001	L	14	10	0.17	0.82	0.414	A
24♀	21	3	0.75	3.67	<0.001	L	18	6	0.50	2.45	0.014	L
25♀	19	5	0.58	2.86	0.004	L	15	9	0.25	1.22	0.221	A
26♀	20	4	0.67	3.27	0.001	L	8	16	-0.33	-1.63	0.102	A
27♀	19	5	0.58	2.86	0.004	L	13	11	0.08	0.41	0.683	A

Red-necked wallabies demonstrated group-level preference of the left forelimb for feeding from the bipedal position (mean HI \pm SEM = 0.45 ± 0.07 ; one-sample Wilcoxon signed-rank test, $W = 302$, $p < 0.001$, $n = 27$) and for autogrooming (mean HI = 0.71 ± 0.09 ; $W = 45$, $p = 0.009$, $n = 9$). In contrast, the group-level preference of the right forelimb for supporting the body in the tripodal stance was found (mean HI = -0.27 ± 0.08 ; $W = -232$, $p = 0.006$,

$n = 27$). No group-level preference was found for feeding from the quadrupedal position (mean HI = 0.08 ± 0.04 ; $W = 109$, $p = 0.120$, $n = 27$; Fig. 16).

Young. In 42 out of the 47 observed instances of suckling, young wallabies, having pulled down the edge of the mother's pouch with both forelimbs, lowered the right forelimb on the ground and continued to pull down the pouch with the left forelimb. Both young wallabies in which individual laterality was assessed preferred to lower the right forelimb on the ground

Table 8.

Individual preferences in forelimb use for supporting of tripedal stance and autogrooming in adult red-necked wallaby, *Macropus (Notamacropus) rufogriseus* in captivity

Subject, sex	Supporting of tripedal stance						Autogrooming					
	L	R	HI	z	p	Pref.	L	R	HI	z	p	Pref.
1♂	6	47	-0.77	-5.63	<0.001	R	9	1	0.80	2.21	0.021	L
2♂	20	33	-0.25	-1.79	0.074	A	8	2	0.60	1.58	0.109	A
3♂	14	39	-0.47	-3.43	<0.001	R	-	-	-	-	-	-
4♂	8	45	-0.70	-5.08	<0.001	R	6	4	0.20	0.32	0.754	A
5♂	21	32	-0.21	-1.51	0.131	A	-	-	-	-	-	-
6♂	13	40	-0.51	-3.71	<0.001	R	-	-	-	-	-	-
7♂	29	24	0.09	0.69	0.492	A	10	0	1.00	2.85	0.002	L
8♂	41	12	0.55	3.98	<0.001	L	-	-	-	-	-	-
9♂	3	50	-0.89	-6.46	<0.001	R	-	-	-	-	-	-
10♂	25	28	-0.06	-0.41	0.680	A	-	-	-	-	-	-
11♂	9	44	-0.66	-4.81	<0.001	R	-	-	-	-	-	-
12♂	51	2	0.92	6.73	<0.001	L	8	2	0.60	1.58	0.109	A
13♂	7	46	-0.74	-5.36	<0.001	R	-	-	-	-	-	-
14♀	15	38	-0.43	-3.16	0.002	R	-	-	-	-	-	-
15♀	10	43	-0.62	-4.53	<0.001	R	10	0	1.00	2.85	0.002	L
16♀	22	31	-0.17	-1.24	0.216	A	7	3	0.40	0.95	0.344	A
17♀	30	23	0.13	0.96	0.336	A	-	-	-	-	-	-
18♀	26	27	-0.02	-0.14	0.890	A	-	-	-	-	-	-
19♀	28	25	0.06	0.41	0.680	A	-	-	-	-	-	-
20♀	11	42	-0.58	-4.26	<0.001	R	-	-	-	-	-	-
21♀	29	24	0.09	0.69	0.492	A	-	-	-	-	-	-
22♀	21	32	-0.21	-1.51	0.131	A	-	-	-	-	-	-
23♀	16	37	-0.40	-2.88	0.004	R	10	0	1.00	2.85	0.002	L
24♀	14	39	-0.47	-3.43	<0.001	R	9	1	0.80	2.21	0.021	L
25♀	12	41	-0.55	-3.98	<0.001	R	-	-	-	-	-	-
26♀	7	46	-0.74	-5.36	<0.001	R	-	-	-	-	-	-
27♀	36	17	0.36	-2.61	0.009	L	-	-	-	-	-	-

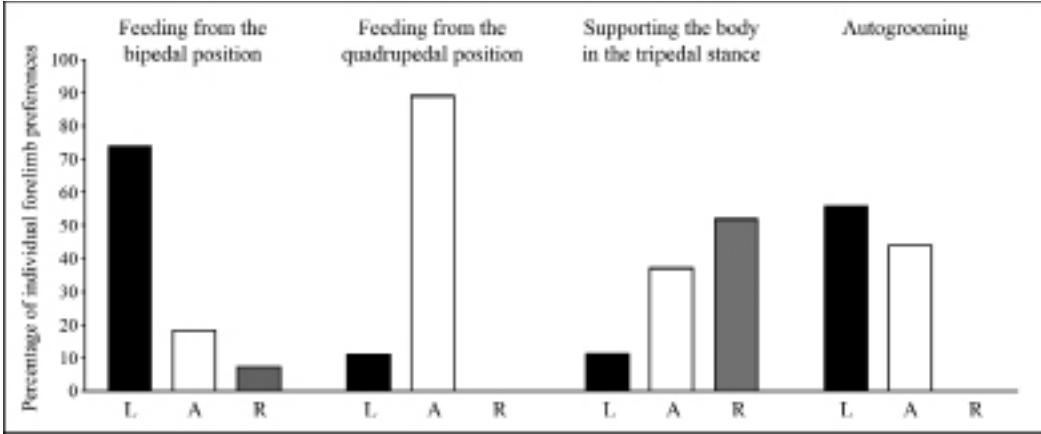


Fig. 15. Individual manual preferences in captive red-necked wallaby. Designations as in Fig. 9. The data from Giljov et al., 2012c.

and to pull down the edge of the mother’s pouch with the left one (10 acts out of the 10 acts recorded, binomial test, $z = 2.85, p = 0.002$ and 11 acts out of the 12 acts recorded, $z = 2.60, p = 0.006$). The other four young wallabies used their forelimbs in this way in 8 out of 8, 4 out of 7, 5 out of 5, and 4 out of 5 recorded acts.

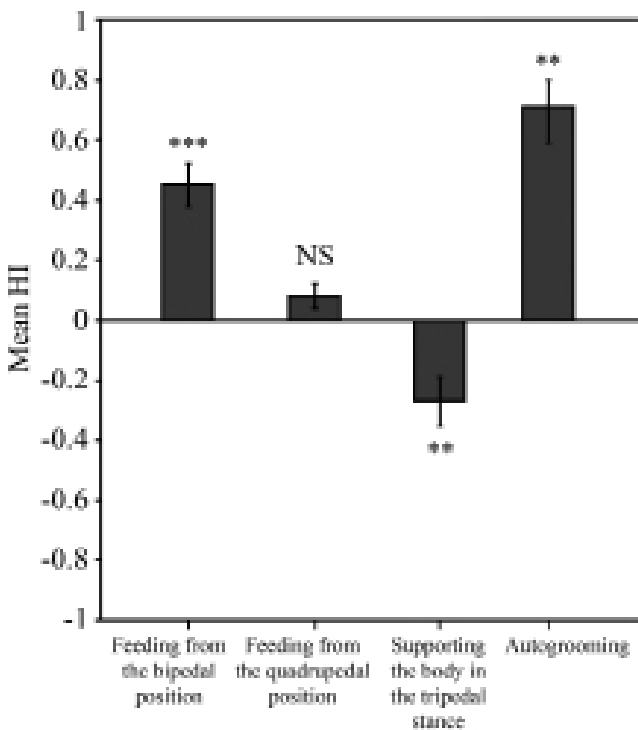


Fig. 16. Group-level laterality in captive red-necked wallaby. Designations as in Fig. 10; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; NS—not significant.

3.4.2. Laterality in wild individuals

3.4.2.1. Unimanual behaviours

Adults. Manual preferences in wild red-necked wallabies were studied for feeding from the bipedal position, feeding from the quadrupedal position, supporting the body in the tripedal stance and autogrooming (Fig. 3a–c) [Giljov et al., 2015a]. The wallabies used one forelimb for feeding on grass, ferns and shoots of shrubs and trees. To assess manual preferences for feeding from the bipedal position, on the average 27 acts of the use of one limb per individual were obtained for 20 individuals (15–42 acts from an individual). For feeding from the quadrupedal position, on the average 24 acts per individual were obtained for 17 individuals (15–34 acts from an individual). Feeding on leaves of shrubs and trees with the use of both forelimbs was studied separately. During this bimanual feeding the wallabies use one forelimb to support the branch at the necessary height and the other one to manipulate leaves and shoots, directing them to the mouth (Fig. 3d). Observing the wallabies, we registered the functions of each forelimb. Since this behaviour was rarely observed twice in the same individual, we did not study individual preferences in this case. Altogether, 42 acts of bimanual feeding from 42 different individuals were registered (one act from an individual).

The use of one forelimb for supporting the body in the tripedal stance and autogrooming (snout cleaning) in wild red-necked wallabies was registered in the same way as in captive individuals (section 3.4.1). For the analysis of forelimb preferences for supporting the body in the tripedal stance, we obtained on the average 28 acts of the use of one forelimb per individual for 18 individuals (17–42 acts from an individual). Manual preferences for autogrooming were studied in 14 red-necked wallabies; on the average 20 acts of the use of one forelimb per individual were obtained (15–33 acts from an individual).

Young. Early manifestations of motor laterality were studied in the red-necked wallaby pouch young. We obtained on the average 22 acts of the use of one forelimb for manipulating plant food from the mother's pouch per individual for 11 pouch young (15–37 acts from an individual). We registered only those cases when both forelimbs had been freed from the pouch before manipulating food. We also registered the cases when the young freed one forelimb together with the head from the mother's pouch (Fig. 4a). On the average 28 acts of freeing one limb per individual were obtained for 10 individuals (15–46 acts from an individual).

3.4.2.2. Distribution of individual preferences and group-level laterality in the use of forelimbs

Adults. For feeding from the bipedal position, 15 wallabies (75%) preferred to use the left forelimb, two individuals (10%) preferred to use the right forelimb, and three (15%) showed no preference (Fig. 17; Table 9). Most individuals were lateralised (binomial test, $z = 2.91$, $p = 0.003$), the number of left-handers among lateralised individuals considerably exceeding that of right-handers ($z = 2.91$, $p = 0.002$).

The left-forelimb preference for feeding from the quadrupedal position was found in 10 wallabies (59%); the right limb preference was found in four individuals (24%); three individuals (18%) showed no preference (Fig. 17; Table 9). Most of the studied individuals

Table 9.

Individual preferences in forelimb use for feeding in adult red-necked wallaby,
Macropus (Notamacropus) rufogriseus in the wild

Subject, sex	Feeding from the bipedal position						Feeding from the quadrupedal position					
	L	R	HI	z	p	Pref.	L	R	HI	z	p	Pref.
1♂	19	5	0.58	2.65	0.007	L	–	–	–	–	–	–
2♂	25	11	0.39	2.17	0.029	L	14	4	0.56	2.12	0.031	L
3♂	10	16	-0.23	-0.59	0.557	A	9	23	-0.44	-2.30	0.020	R
4♂	–	–	–	–	–	–	6	21	-0.56	-2.69	0.006	R
5♂	17	0	1.00	3.88	<0.001	L	25	4	0.72	3.71	<0.001	L
6♂	13	15	-0.07	-0.19	0.851	A	10	5	0.33	1.03	0.302	A
7♂	25	6	0.61	3.23	<0.001	L	19	6	0.52	2.40	0.015	L
8♂	14	2	0.75	2.58	0.007	L	–	–	–	–	–	–
9♂	35	7	0.67	4.17	<0.001	L	26	8	0.53	2.92	0.003	L
10♀	27	6	0.64	3.48	<0.001	L	–	–	–	–	–	–
11♀	–	–	–	–	–	–	14	3	0.65	2.43	0.013	L
12♀	21	5	0.62	2.94	0.002	L	0	17	-1.00	3.88	<0.001	R
13♀	3	16	-0.68	-2.75	0.004	R	–	–	–	–	–	–
14♀	21	14	0.20	1.01	0.311	A	–	–	–	–	–	–
15♀	20	2	0.82	3.62	<0.001	L	21	5	0.62	2.94	0.002	L
16♀	–	–	–	–	–	–	7	15	-0.36	-1.49	0.134	A
17♀	17	2	0.79	3.21	<0.001	L	12	3	0.60	2.07	0.035	L
18♀	25	3	0.79	3.97	<0.001	L	29	4	0.76	4.18	<0.001	L
19♀	28	10	0.47	2.76	0.005	L	–	–	–	–	–	–
20♀	29	5	0.71	3.94	<0.001	L	15	10	0.20	0.80	0.424	A
21♀	9	22	-0.42	-2.16	0.029	R	2	27	-0.86	4.46	<0.001	R
22♀	15	0	1.00	3.61	<0.001	L	13	3	0.63	2.25	0.021	L
23♀	23	4	0.70	3.46	<0.001	L	17	4	0.62	2.62	0.007	L

were lateralised (binomial test, $z = 2.43$, $p = 0.013$), but the number of left-handers did not differ significantly from that of right-handers ($z = 1.34$, $p = 0.180$).

Most red-necked wallabies, in which bimanual feeding on shrubs and trees was observed, supported the branch at the necessary height with the right forelimb, while directed stems to the mouth with the left one (35 observations out of 42; binomial test, $z = 4.17$, $p < 0.001$).

The left-forelimb preference for supporting the body in the tripodal stance was found only in one individual (6%), 13 wallabies (72%) used the right forelimb considerably more often, while four individuals (22%) showed no preference (Fig. 17; Table 10). The number of lateralised individuals exceeded significantly that of non-lateralised ones (binomial test, $z = 2.12$,

$p = 0.031$), with most of the lateralised wallabies preferring to support the body with the right forelimb ($z = -2.94, p = 0.002$).

The left-forelimb preference for autogrooming was found in 13 individuals (93%); one individual (7%) showed no preference (Table 10). Most individuals were lateralised (binomial test, $z = 2.94, p = 0.002$), and most of the lateralised individuals were left-handed ($z = 3.33, p < 0.001$).

Red-necked wallabies showed the group-level left-forelimb preference for feeding from the bipedal position (mean HI \pm SEM = 0.47 ± 0.10 ; one-sample Wilcoxon signed-rank test, $W = 168, p < 0.001, n = 20$) and for autogrooming (mean HI = 0.70 ± 0.05 ; $W = 105, p < 0.001, n = 14$). The right-forelimb preference was found for supporting the body in the tripodal stance (mean HI = -0.39 ± 0.10 ; $W = -139, p = 0.001, n = 18$). No group-level preference was found for feeding from the quadrupedal position (mean HI = 0.21 ± 0.14 ; $W = 58, p = 0.178, n = 17$; Fig. 18).

Table 10.

Individual preferences in forelimb use for supporting of tripodal stance and autogrooming in adult red-necked wallaby, *Macropus (Notamacropus) rufogriseus* in the wild

Subject, sex	Supporting of tripodal stance						Autogrooming					
	L	R	HI	z	p	Pref.	L	R	HI	z	p	Pref.
1♂	2	16	-0.78	-3.06	0.001	R	-	-	-	-	-	-
2♂	8	33	-0.61	-3.75	<0.001	R	14	2	0.75	2.75	0.004	L
3♂	11	12	-0.04	0.00	1.000	A	-	-	-	-	-	-
4♂	6	30	-0.67	-3.83	<0.001	R	-	-	-	-	-	-
5♂	16	5	0.52	2.18	0.027	L	15	0	1.00	3.61	<0.001	L
6♂	-	-	-	-	-	-	18	3	0.71	3.06	0.001	L
7♂	7	27	-0.59	-3.26	<0.001	R	16	3	0.68	2.75	0.019	L
8♂	3	14	-0.65	-2.43	0.013	R	13	2	0.73	3.61	0.007	L
9♂	-	-	-	-	-	-	-	-	-	-	-	-
10♀	11	28	-0.44	-2.56	0.009	R	22	6	0.57	2.83	0.004	L
11♀	-	-	-	-	-	-	-	-	-	-	-	-
12♀	-	-	-	-	-	-	18	4	0.64	2.77	0.004	L
13♀	-	-	-	-	-	-	12	3	0.60	2.07	0.035	L
14♀	13	8	0.24	0.87	0.383	A	-	-	-	-	-	-
15♀	11	26	-0.41	-2.30	0.020	R	15	2	0.76	2.91	0.002	L
16♀	11	24	-0.37	-2.03	0.041	R	13	6	0.37	1.38	0.167	A
17♀	12	6	0.33	1.18	0.238	A	15	0	1.00	3.61	<0.001	L
18♀	-	-	-	-	-	-	20	6	0.54	2.55	0.009	L
19♀	2	17	-0.79	3.21	<0.001	R	-	-	-	-	-	-
20♀	6	22	-0.57	2.83	0.004	R	-	-	-	-	-	-
21♀	18	24	-0.14	2.31	0.441	A	23	10	0.39	2.09	0.035	L
22♀	3	19	-0.73	3.20	<0.001	R	-	-	-	-	-	-
23♀	10	29	-0.49	2.88	0.003	R	18	0	1.00	4.01	<0.001	L
24♀	2	15	-0.76	2.91	0.002	R	-	-	-	-	-	-

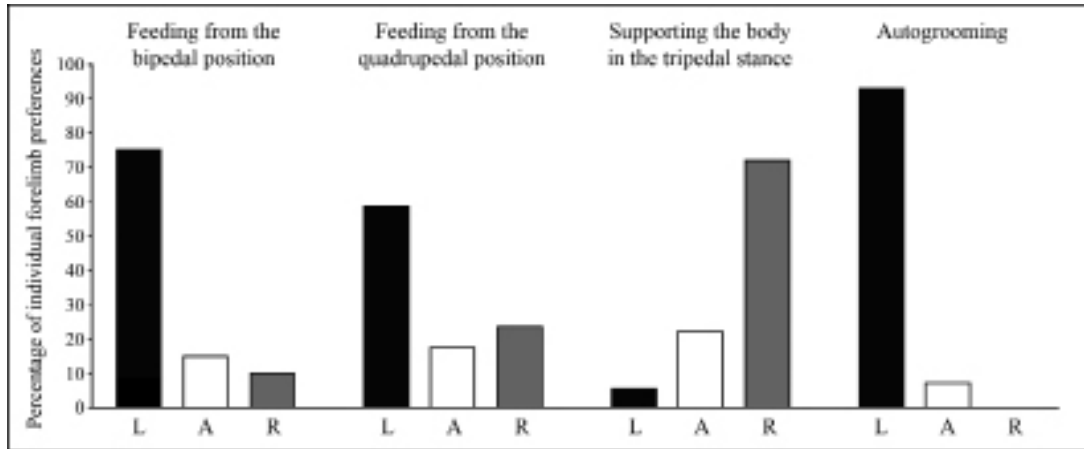


Fig. 17. Individual manual preferences in wild red-necked wallaby. Designations as in Fig. 9.

Young. Seven pouch young wallabies (64%) showed left-forelimb preferences for manipulating food objects, one individual (9%) showed the right-forelimb preference, in three pouch young (27%) no preference was found. No preference for freeing one limb from the mother's pouch was found in eight individuals (80%), and only two young were lateralised for this behaviour. One of them (10%) freed the left forelimb more often, while the other (10%) preferred to free the right forelimb (Table 11).

Table 11.

Individual preferences in forelimb use for manipulating food objects and extending a forelimb out of the mother's pouch in pouch-young red-necked wallaby, *Macropus (Notamacropus) rufogriseus* in the wild

Subject	Manipulating food objects						Extending a forelimb out of the mother's pouch					
	L	R	HI	z	p	Pref.	L	R	HI	z	p	Pref.
1	14	1	0.87	3.1	<0.001	L	8	12	-0.20	-0.67	0.503	A
2	28	6	0.65	3.6	<0.001	L	23	18	0.12	0.62	0.533	A
3	6	9	-0.20	-0.52	0.607	A	11	7	0.22	0.71	0.481	A
4	15	5	0.50	2.01	0.041	L	14	13	0.04	0.00	1.000	A
5	16	0	1.00	3.75	<0.001	L	19	23	-0.10	0.46	0.644	A
6	11	8	0.16	0.46	0.648	A	26	20	0.13	0.74	0.461	A
7	3	13	-0.63	-2.25	0.021	R	5	21	-0.62	2.94	0.002	R
8	19	8	0.41	1.92	0.052	L	9	6	0.20	0.52	0.607	A
9	14	4	0.56	2.12	0.031	L	-	-	-	-	-	-
10	27	10	0.46	2.63	0.008	L	12	12	0.00	0.00	1.000	A
11	23	5	0.64	3.21	<0.001	A	19	4	0.65	2.92	0.003	L

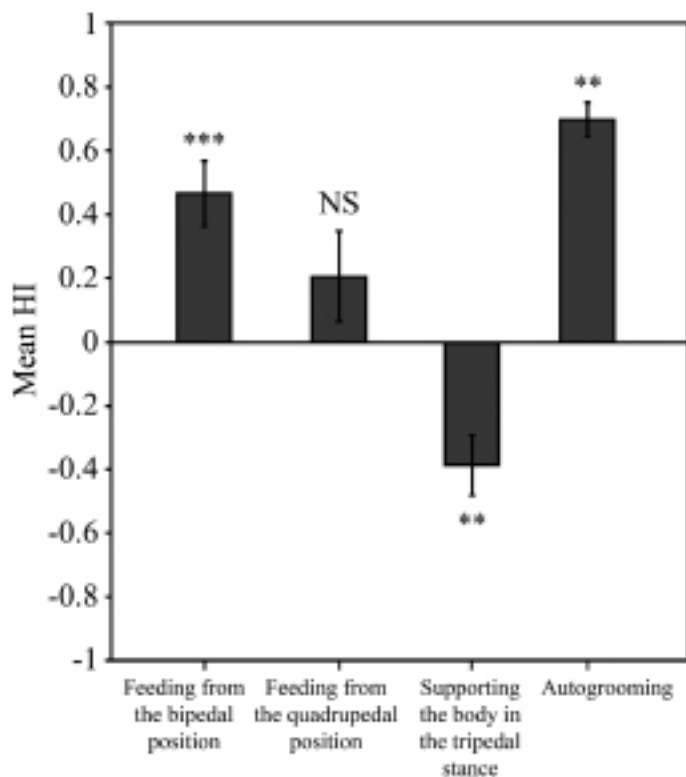
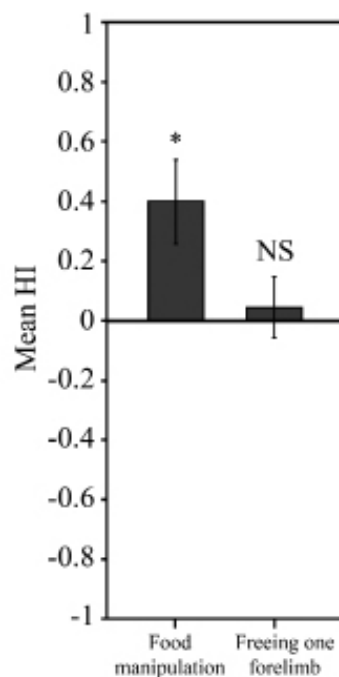


Fig. 18. Group-level laterality in wild red-necked wallabies. Designations as in Fig. 16.

Fig. 19. Group-level manual laterality in the young red-necked wallaby in the wild. Food manipulation and freeing one forelimb from the mother's pouch was studied in pouch young. Designations as in Fig. 16.



The young of the red-necked wallaby showed the group-level left-forelimb preference for manipulating food objects (mean HI = 0.40 ± 0.14 ; one-sample Wilcoxon signed-rank test, $W = 48$, $p = 0.032$, $n = 11$) but no group-level preference was found for freeing one paw from the mother's pouch (mean HI = 0.05 ± 0.10 ; $W = 14$, $p = 0.426$, $n = 10$; Fig. 19 [Giljov et al., 2017]).

3.4.2.3. Assessment of manual laterality by route surveys

During the analysis of data obtained by the route survey technique, only one act of forelimb use in each behaviour was registered from each individual encountered on the route. Comparison of the data obtained in two sites of data collection at Maria Island, did not reveal any statistically significant differences for any of the behaviours ($p > 0.05$, Z-test for proportions) and therefore the data were pooled. The left-forelimb preference was found for feeding from the bipedal position (56 observations of the use of the left forelimb out of 80; binomial test, $z = 3.47$, $p < 0.001$) and for autogrooming (25 observations of the use of the left forelimb out of 37; $z = 1.97$, $p = 0.047$). In most cases wallabies used the right forelimb for supporting the body in the tripedal stance (82 observations of the use of the right forelimb out of 121; binomial test, $z = 3.82$, $p < 0.001$). For feeding from the quadrupedal position, the number of registered acts of the left forelimb use did not differ significantly from that of the right forelimb use (79 observations of the use of the left forelimb out of 145; binomial test, $z = 1.00$, $p = 0.319$).

3.5. Manual laterality in the eastern grey kangaroo, *Macropus (Macropus) giganteus*

3.5.1. Laterality in captive individuals

3.5.1.1. Unimanual behaviours

Adults. Manual preferences in adult eastern grey kangaroos were studied for feeding from the bipedal position, feeding from the quadrupedal position, supporting the body in the tripedal stance (Fig. 3) and autogrooming. The characteristics of these behaviours were the same as in red-necked wallabies. For the analysis of manual preferences for feeding from the bipedal position, on the average 42 acts of the use of one limb per individual were obtained for 33 individuals (31–65 acts from an individual). To assess manual preferences for feeding from the quadrupedal position, we obtained on the average 44 acts per individual for 34 individuals (32–61 acts from an individual). For supporting the body in the tripedal stance, on the average 48 acts of the use of one limb per individual were obtained for 28 individuals (32–74 acts from an individual; $n = 28$). For autogrooming, on the average 40 acts of the use of one forelimb per individual were obtained for 15 individuals (32–54 acts from an individual).

Young. Forelimb preferences of 12 young-at-foot eastern grey kangaroo were studied during milk suckling [Giljov et al., 2017]. After pulling the edge of the pouch with both paws, they often put one paw out of the pouch and continued to pull down the edge with the other one. In contrast to red-necked wallabies, young-at-foot eastern grey kangaroos did not use the freed forelimb for supporting the body but let it hang in the air (Fig. 4c). This difference between the two species is apparently associated with a stronger disproportion of forelimbs and hind limbs in kangaroos as compared to wallabies [Hume et al., 1989]. On the average 23 acts of the use of one limb during suckling per individual were obtained for 12 young kangaroos (32–74 acts from an individual).

Early manifestations of manual laterality were recorded in eight pouch young eastern grey kangaroo. A typical behaviour of the young kangaroos from the fifth month of life is freeing

the head and the forepaws from the mother's pouch; as it does so, the young often tries food objects within its reach [Dawson, 2012]. For the analysis of lateralised forelimb use for manipulation of food objects by pouch young, on the average 21 acts of the use of one forelimb to take up mown grass from the ground per individual were obtained for eight individuals (15–28 acts from an individual). We registered only those cases when the young freed both forelimbs before manipulating food from the pouch (Fig. 4b).

Besides, asymmetrical freeing of forepaws from the mother's pouch was studied (Fig. 4a). When putting out the head from the pouch, the young often also freed one of the forepaws. On the average 27 acts of freeing one limb from the mother's pouch per individual were obtained for eight individuals (16–36 acts from an individual).

3.5.1.2. Distribution of individual and group-level manual preferences

Adults. The left-forelimb preference for feeding from the bipedal position was found in 26 individuals (79%), the right-forelimb preference was found in three individuals (9%), and four kangaroos (12%) showed no preference (Fig. 20; Table 12). The number of lateralised individuals was considerably greater than that of non-lateralised ones (binomial test, $z = 4.18$, $p < 0.001$), and the number of left-handers considerably exceeded the number of right-handers ($z = 4.04$, $p < 0.001$).

The left-forelimb preference for feeding from the quadrupedal position was found for 21 individuals (62%), two individuals (6%) preferred to use the right forelimb, and 11 kangaroos (32%) showed no forelimb preference (Fig. 20; Table 12). The number of lateralised individuals did not differ significantly from that of non-lateralised ones (binomial test, $z = 1.89$, $p = 0.058$), but the number of left-handers among lateralised individuals exceeded considerably that of right-handers ($z = 3.75$, $p < 0.001$).

The left-forelimb preference for supporting the body in the tripedal stance was found in 17 individuals (61%); four individuals (14%) preferred to use the right forelimb; in seven kangaroos (25%) no manual preference was found (Fig. 20; Table 13). The number of lateral-

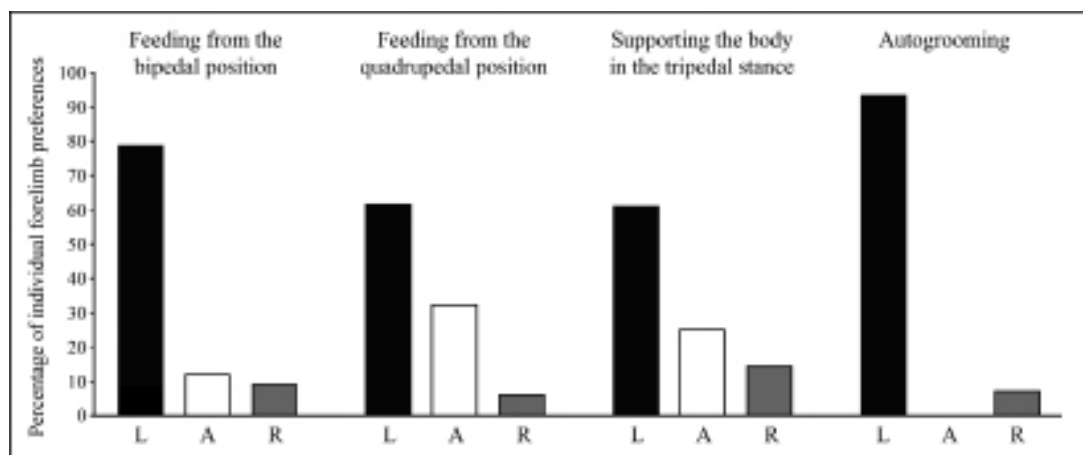


Fig. 20. Individual manual preferences in captive eastern grey kangaroo. Designations as in Fig. 9.

Table 12.

Individual preferences in forelimb use for feeding in adult eastern grey kangaroo,
Macropus (M.) giganteus in captivity

Subject, sex	Feeding from the bipedal position						Feeding from the quadrupedal position					
	L	R	HI	z	p	Pref.	L	R	HI	z	p	Pref.
1♂	43	4	0.83	5.54	<0.001	L	29	6	0.66	3.72	<0.001	L
2♂	39	12	0.53	3.64	<0.001	L	30	17	0.28	1.75	0.080	A
3♂	27	5	0.69	3.71	<0.001	L	20	32	-0.23	-1.53	0.126	A
4♂	13	31	-0.41	-2.56	0.010	R	41	8	0.67	4.57	<0.001	L
5♂	24	15	0.23	1.28	0.200	A	26	12	0.37	2.11	0.034	L
6♂	40	8	0.67	4.47	<0.001	L	35	16	0.37	2.52	0.011	L
7♂	38	3	0.85	5.31	<0.001	L	42	10	0.62	4.30	<0.001	L
8♂	26	7	0.58	3.13	0.001	L	18	22	-0.10	-0.47	0.636	A
9♂	47	18	0.45	3.47	<0.001	L	38	14	0.46	3.19	0.001	L
10♂	30	5	0.71	4.06	<0.001	L	49	12	0.61	4.61	<0.001	L
11♂	37	16	0.40	2.75	0.005	L	25	16	0.22	1.25	0.211	L
12♂	34	7	0.66	4.06	<0.001	L	29	5	0.71	3.94	<0.001	L
13♂	26	9	0.49	2.70	0.006	L	37	17	0.37	2.59	0.009	L
14♀	35	15	0.40	2.69	0.007	L	31	11	0.48	2.93	0.003	L
15♀	33	0	1.00	5.57	<0.001	L	26	12	0.37	2.11	0.034	L
16♀	–	–	–	–	–	–	19	17	0.06	0.17	0.868	A
17♀	14	32	-0.39	-2.51	0.011	R	6	32	-0.68	-4.06	<0.001	R
18♀	29	9	0.53	3.08	0.002	L	43	14	0.51	3.71	<0.001	L
19♀	31	6	0.68	3.95	<0.001	L	26	6	0.63	3.36	<0.001	L
20♀	24	16	0.20	1.11	0.268	A	19	16	0.09	0.34	0.736	A
21♀	40	9	0.63	4.29	<0.001	L	41	14	0.49	3.51	<0.001	L
22♀	26	11	0.41	2.30	0.020	L	14	20	-0.18	-0.86	0.392	A
23♀	52	6	0.79	5.91	<0.001	L	38	16	0.41	2.86	0.004	L
24♀	28	4	0.75	4.07	<0.001	L	26	10	0.44	2.50	0.011	L
25♀	32	7	0.64	3.84	<0.001	L	31	12	0.44	2.74	0.005	L
26♀	29	2	0.87	4.67	<0.001	L	34	2	0.89	5.17	<0.001	L
27♀	26	16	0.24	1.39	0.164	A	33	15	0.38	2.45	0.014	L
28♀	11	27	-0.42	-2.43	0.014	R	27	17	0.23	1.36	0.174	A
29♀	41	13	0.52	3.67	<0.001	L	36	21	0.26	1.85	0.063	A
30♀	33	2	0.89	4.39	<0.001	L	27	10	0.46	2.63	0.008	L
31♀	28	9	0.51	2.96	0.003	L	12	34	-0.48	-3.10	0.002	R
32♀	39	10	0.59	4.00	<0.001	L	27	26	0.02	0.00	1.000	A
33♀	32	4	0.78	4.50	<0.001	L	29	10	0.49	2.88	0.003	L
34♀	22	12	0.29	1.54	0.121	A	25	16	0.22	1.25	0.211	A

used individuals exceeded that of non-lateralised ones (binomial test, $z = 2.46$, $p = 0.013$), and the number of left-handers exceeded considerably that of right-handers ($z = 2.62$, $p = 0.007$).

The left-forelimb preference for autogrooming was found in 14 individuals (93%), while the right-forelimb preference was recorded only in one individual (7%) (Fig. 20; Table 13). All individuals were lateralised (binomial test, $z = 3.61$, $p < 0.001$). The number of left-handers was significantly greater than that of right-handers ($z = 3.10$, $p < 0.001$).

Eastern grey kangaroos showed the group-level left-forelimb preference in all the behaviours: feeding from the bipedal position (mean HI \pm SEM = 0.50 ± 0.06 ; one-sample Wilcoxon signed-rank test, $W = 513$, $p < 0.001$, $n = 33$), feeding from the quadrupedal position (mean HI = 0.31 ± 0.06 ; $W = 449$, $p < 0.001$, $n = 34$), supporting the body in the tripedal stance (mean HI = 0.22 ± 0.07 ; $W = 250$, $p = 0.005$, $n = 28$) and autogrooming (mean HI = 0.51 ± 0.10 ; $W = 94$, $p = 0.008$, $n = 15$; Fig. 21).

Table 13.

Individual preferences in forelimb use for supporting of tripedal stance and autogrooming in adult eastern grey kangaroo, *Macropus (M.) giganteus* in captivity

Subject, sex	Supporting of tripedal stance						Autogrooming					
	L	R	HI	z	p	Pref.	L	R	HI	z	p	Pref.
1♂	42	15	0.47	3.44	<0.001	L	–	–	–	–	–	–
2♂	31	14	0.38	2.39	0.016	L	29	6	0.66	3.72	<0.001	L
3♂	26	6	0.63	3.36	<0.001	L	32	9	0.56	3.44	<0.001	L
4♂	44	18	0.42	3.18	0.001	L	–	–	–	–	–	–
5♂	26	29	–0.05	–0.27	0.788	A	–	–	–	–	–	–
6♂	40	17	0.40	2.91	0.003	L	26	6	0.63	3.36	<0.001	L
7♂	38	16	0.41	2.86	0.004	L	34	0	1.00	5.66	<0.001	L
8♂	9	24	–0.45	–2.44	0.014	R	–	–	–	–	–	–
9♂	25	17	0.19	–1.08	0.280	A	38	15	0.43	3.02	0.002	L
10♂	36	5	0.76	4.69	<0.001	L	–	–	–	–	–	–
11♂	27	16	0.26	1.52	0.126	A	27	11	0.42	2.43	0.014	L
12♂	14	33	–0.40	–2.63	0.008	R	–	–	–	–	–	–
13♂	–	–	–	–	–	–	–	–	–	–	–	–
14♀	29	8	0.57	3.29	<0.001	L	39	8	0.66	4.38	<0.001	L
15♀	34	17	0.33	2.24	0.024	L	28	7	0.60	3.38	<0.001	L
16♀	–	–	–	–	–	–	–	–	–	–	–	–
17♀	43	19	0.39	2.92	0.003	L	7	44	–0.73	–5.04	<0.001	R
18♀	37	11	0.54	3.61	<0.001	L	26	6	0.63	3.36	<0.001	L
19♀	–	–	–	–	–	–	–	–	–	–	–	–
20♀	14	36	–0.44	–2.97	0.003	R	–	–	–	–	–	–
21♀	28	10	0.47	2.76	0.005	L	31	8	0.59	3.52	<0.001	L
22♀	22	34	–0.21	–1.47	0.141	A	–	–	–	–	–	–
23♀	30	11	0.46	2.81	0.004	L	34	6	0.70	4.27	<0.001	L
24♀	46	17	0.46	3.53	<0.001	L	–	–	–	–	–	–
25♀	14	19	–0.15	–0.70	0.487	A	–	–	–	–	–	–
26♀	43	31	0.16	1.28	0.201	L	–	–	–	–	–	–
27♀	–	–	–	–	–	–	–	–	–	–	–	–
28♀	18	41	–0.39	–2.86	0.004	R	29	14	0.35	2.13	0.032	L
29♀	27	9	0.50	2.83	0.004	L	30	3	0.82	4.53	<0.001	L
30♀	–	–	–	–	–	–	–	–	–	–	–	–
31♀	39	22	0.28	2.05	0.040	L	–	–	–	–	–	–
32♀	31	9	0.55	3.32	<0.001	L	37	17	0.37	2.59	0.009	L
33♀	–	–	–	–	–	–	–	–	–	–	–	–
34♀	11	23	–0.35	1.89	0.058	A	–	–	–	–	–	–

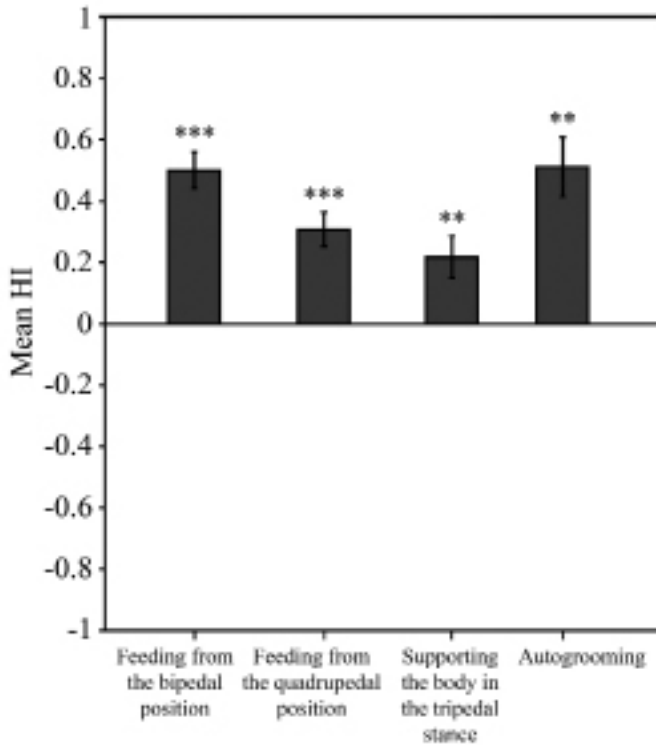


Fig. 21. Group-level manual laterality in captive eastern grey kangaroo. Designations as in Fig. 16.

Young. The analysis of the data on the young-at-foot showed that 10 of them (83%) preferred to use the left paw for pulling down the mother's pouch during suckling, while the remaining two (7%) showed no preference (Table 14). The number of lateralised individuals was

Table 14.

Individual preferences in forelimb use for manipulating mother's pouch edge during milk suckling in young-at-foot eastern grey kangaroo, *Macropus (M.) giganteus* in captivity

Subject	Manipulating mother's pouch edge					
	L	R	HI	z	p	Pref.
1	17	6	0.48	2.09	0.035	L
2	11	4	0.47	1.55	0.118	A
3	22	6	0.57	2.83	0.004	L
4	26	10	0.44	2.50	0.011	L
5	16	0	1.00	3.75	<0.001	L
6	21	3	0.75	3.47	<0.001	L
7	5	13	-0.44	-1.65	0.096	A
8	18	5	0.57	2.50	0.011	L
9	14	3	0.65	2.43	0.013	L
10	24	6	0.60	3.10	0.001	L
11	17	2	0.79	3.21	<0.001	L
12	18	7	0.44	2.00	0.043	L

considerably greater than that of non-lateralised ones (binomial test, $z = 2.02$, $p = 0.039$), and the number of left-handers exceeded considerably that of right-handers ($z = 2.85$, $p = 0.002$). The left-forelimb preference in the young was also revealed at the level of the group (mean HI = 0.53 ± 0.10 ; one-sample Wilcoxon signed-rank test, $W = 73$, $p = 0.005$, $n = 12$; Fig. 22).

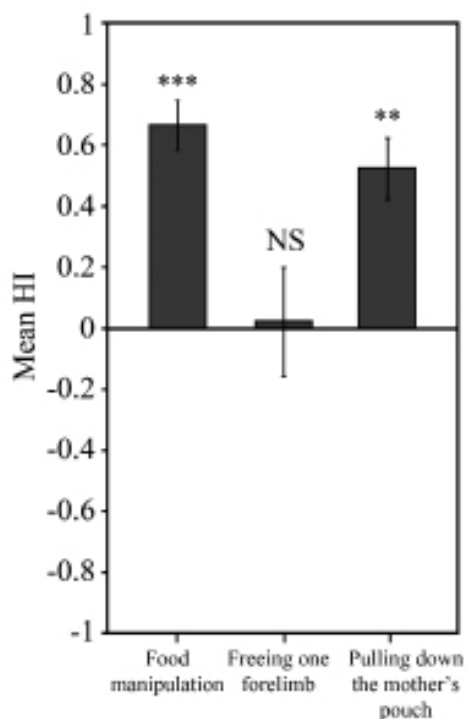


Fig. 22. Group-level laterality in the young of the eastern grey kangaroo in captivity. Food manipulation and freeing of one forelimb from the mother's pouch was studied in pouch young; pulling down the mother's pouch during suckling was studied in young-at-foot. Designations as in Fig. 16.

Table 15.

Individual preferences in forelimb use for manipulating food objects and extending a forelimb out of the mother's pouch in pouch-young eastern grey kangaroo, *Macropus (M.) giganteus* in captivity

Subject	Manipulating food objects						Extending a forelimb out of the mother's pouch					
	L	R	HI	z	p	Pref.	L	R	HI	z	p	Pref.
1	21	4	0.68	3.20	<0.001	L	13	21	-0.24	-1.20	0.229	A
2	15	2	0.76	2.91	0.002	L	26	10	0.44	2.50	0.011	L
3	19	3	0.73	3.20	<0.001	L	22	5	0.63	3.08	0.002	L
4	20	8	0.43	2.08	0.036	L	15	7	0.36	1.49	0.134	A
5	13	2	0.73	2.58	0.007	L	12	16	-0.14	-0.57	0.572	A
6	15	9	0.25	1.02	0.307	A	11	5	0.38	1.25	0.21	A
7	18	0	1.00	4.01	<0.001	L	2	19	-0.81	-1.08	0.281	A
8	15	2	0.76	2.91	0.002	L	5	13	-0.44	-1.65	0.096	A

Seven pouch young (87%) showed the left-forelimb preference for manipulating food, while one individual (13%) showed no preference. The analysis of cases when the young freed one forelimb from the mother's pouch showed that two individuals (25%) considerably more often freed the left forelimb, while the remaining six individuals (75%) showed no preference (Table 15).

In the young of the eastern grey kangaroo, we found a group-level left-forelimb preference for manipulating food objects (mean HI \pm SEM = 0.67 ± 0.08 ; one-sample Wilcoxon signed-rank test, $W = 36$, $p = 0.008$, $n = 8$; Fig. 11), but no group-level laterality for simple freeing of one forelimb from the mother's pouch was revealed (mean HI = 0.02 ± 0.18 ; $W = 3$, $p = 0.844$, $n = 8$; Fig. 22 [Giljov et al., 2017]).

3.5.2. Laterality in wild individuals

3.5.2.1. Unimanual behaviours

In wild adult eastern grey kangaroos the same behaviours were studied as in captive individuals of this species [Giljov et al., 2015a]. To assess manual preferences for feeding on grass, on the average 22 acts of the use of one forelimb from the bipedal position per individual were obtained for 19 individuals (15–33 acts from an individual) and on the average 24 acts of the use of one forelimb from the quadrupedal position per individual were obtained for 22 individuals (15–39 acts from an individual).

For the analysis of manual preferences for supporting the body in the tripedal stance, on the average 25 acts of the use of one forelimb per individual were obtained for 25 individuals (16–39 acts from an individual). For autogrooming, on the average 24 acts per individual were obtained for 29 individuals (15–37 acts from an individual; $n = 29$).

3.5.2.2. Distribution of individual preferences and group-level laterality in the use of forelimbs

The left-forelimb preference for feeding from the bipedal position was found in 15 eastern grey kangaroos (79%); the right-forelimb preference was observed in one individual (5%); three individuals (16%) showed no individual preferences (Fig. 23; Table 16). The number of lateralised individuals was considerably greater than that of non-lateralised ones (binomial test, $z = 2.75$, $p = 0.004$). The number of left-handers exceeded that of right-handers ($z = 3.25$, $p < 0.001$). For feeding from the quadrupedal position, 14 individuals (64%) preferred to use the left forelimb, three individuals (13%) preferred to use the right forelimb, and five individuals (23%) showed no preference (Fig. 23; Table 16). The number of lateralised individuals considerably exceeded that of non-lateralised ones (binomial test, $z = 2.35$, $p = 0.017$). The number of left-handers was greater than that of right-handers ($z = 2.43$, $p = 0.013$).

The left-forelimb preference for supporting the body in the tripedal stance was found in 15 eastern grey kangaroos (60%), the right-forelimb preference was found in four individuals (16%), and six individuals (24%) showed no preference (Fig. 23; Table 17). The number of lateralised individuals considerably exceeded that of non-lateralised ones (binomial test, $z = 2.40$, $p = 0.015$), and the number of left-handers was considerably greater than that of right-handers ($z = 2.29$, $p = 0.019$).

Table 16.

Individual preferences in forelimb use for feeding in adult eastern grey kangaroo, *Macropus (M.) giganteus* in the wild

Subject, sex	Feeding from the bipedal position						Feeding from the quadrupedal position					
	L	R	HI	z	p	Pref.	L	R	HI	z	p	Pref.
1♂	–	–	–	–	–	–	15	0	1.00	3.61	<0.001	L
2♂	–	–	–	–	–	–	–	–	–	–	–	–
3♂	17	6	0.48	2.09	0.035	L	8	13	–0.24	0.87	0.383	A
4♂	18	0	1.00	4.01	<0.001	L	–	–	–	–	–	–
5♂	20	4	0.67	3.06	0.002	L	25	7	0.56	3.01	0.002	L
6♂	–	–	–	–	–	–	14	4	0.56	2.12	0.031	L
7♂	–	–	–	–	–	–	–	–	–	–	–	–
8♂	7	11	–0.22	–0.71	0.481	A	6	19	–0.52	2.40	0.015	R
9♂	14	1	0.87	3.10	0.001	L	–	–	–	–	–	–
10♂	–	–	–	–	–	–	16	3	0.68	2.75	0.004	L
11♂	21	6	0.56	2.69	0.006	L	–	–	–	–	–	–
12♂	–	–	–	–	–	–	21	6	0.56	2.69	0.006	L
13♀	12	10	0.09	0.21	0.832	A	5	13	–0.44	0.64	0.523	A
14♀	26	7	0.58	3.13	0.001	L	–	–	–	–	–	–
15♀	–	–	–	–	–	–	23	8	0.48	2.51	0.011	L
16♀	–	–	–	–	–	–	–	–	–	–	–	–
17♀	16	4	0.60	2.46	0.012	L	–	–	–	–	–	–
18♀	–	–	–	–	–	–	21	9	0.40	2.01	0.043	L
19♀	7	11	–0.22	0.71	0.481	A	10	14	–0.17	0.61	0.541	A
20♀	–	–	–	–	–	–	–	–	–	–	–	–
21♀	19	5	0.58	2.65	0.007	L	26	9	0.49	2.70	0.006	L
22♀	17	2	0.79	3.21	0.001	L	–	–	–	–	–	–
23♀	20	8	0.43	2.08	0.036	L	2	14	–0.75	–2.75	0.004	R
24♀	–	–	–	–	–	–	–	–	–	–	–	–
25♀	–	–	–	–	–	–	19	6	0.52	2.40	0.015	L
26♀	–	–	–	–	–	–	14	8	0.27	1.07	0.286	A
27♀	–	–	–	–	–	–	12	3	0.60	2.07	0.035	L
28♀	16	5	0.52	2.18	0.027	L	15	11	0.15	0.59	0.557	A
29♀	–	–	–	–	–	–	–	–	–	–	–	–
30♀	22	6	0.57	2.83	0.004	L	–	–	–	–	–	–
31♀	–	–	–	–	–	–	23	7	0.53	2.74	0.005	L
32♀	17	0	1.00	3.88	<0.001	L	–	–	–	–	–	–
33♀	–	–	–	–	–	–	18	7	0.44	2.00	0.043	L
34♀	3	15	–0.67	–2.59	0.008	R	5	16	–0.52	–2.18	0.023	R
35♀	23	7	0.53	2.74	0.005	L	29	10	0.49	2.88	0.003	L
36♀	–	–	–	–	–	–	–	–	–	–	–	–
37♀	–	–	–	–	–	–	14	3	0.65	2.43	0.013	L
38♀	13	2	0.73	2.58	0.007	L	–	–	–	–	–	–

Table 17.

Individual preferences in forelimb use for supporting of tripodal stance and autogrooming in adult eastern grey kangaroo, *Macropus (M.) giganteus* in the wild

Subject, sex	Supporting of tripodal stance						Autogrooming					
	L	R	HI	<i>z</i>	<i>p</i>	Pref.	L	R	HI	<i>z</i>	<i>p</i>	Pref.
1♂	16	3	0.68	2.75	0.004	L	–	–	–	–	–	–
2♂	–	–	–	–	–	–	23	14	0.24	1.32	0.188	A
3♂	12	8	0.20	0.067	0.503	A	23	8	0.48	2.51	0.011	L
4♂	–	–	–	–	–	–	16	4	0.60	2.46	0.012	L
5♂	17	1	0.89	3.54	<0.001	L	–	–	–	–	–	–
6♂	22	9	0.42	2.16	0.029	L	18	1	0.89	3.67	<0.001	L
7♂	3	13	–0.63	2.25	0.021	R	15	3	0.67	2.07	0.035	L
8♂	–	–	–	–	–	–	12	19	–0.23	1.08	0.281	A
9♂	20	6	0.54	2.55	0.009	L	–	–	–	–	–	–
10♂	–	–	–	–	–	–	19	1	0.90	3.80	<0.001	L
11♂	13	3	0.63	2.25	0.021	L	20	8	0.43	2.08	0.036	L
12♂	27	12	0.38	2.24	0.023	L	22	9	0.42	2.16	0.029	L
13♀	–	–	–	–	–	–	21	7	0.50	2.60	0.008	L
14♀	21	6	0.56	2.69	0.006	L	18	6	0.50	2.25	0.023	L
15♀	–	–	–	–	–	–	12	14	–0.08	0.20	0.845	A
16♀	14	4	0.56	2.12	0.031	L	–	–	–	–	–	–
17♀	15	10	0.20	0.80	0.424	A	–	–	–	–	–	–
18♀	26	9	0.49	2.70	0.006	L	15	3	0.67	2.07	0.035	L
19♀	8	22	–0.47	2.37	0.016	R	10	5	0.33	1.03	0.302	A
20♀	16	5	0.52	2.18	0.027	L	–	–	–	–	–	–
21♀	20	8	0.43	2.08	0.036	L	17	4	0.62	2.62	0.007	L
22♀	–	–	–	–	–	–	5	19	–0.58	2.65	0.007	R
23♀	17	12	0.17	1.15	0.248	A	17	0	1.00	3.88	<0.001	L
24♀	5	19	–0.58	2.65	0.007	R	8	21	–0.45	2.23	0.024	R
25♀	–	–	–	–	–	–	15	3	0.67	2.59	0.008	L
26♀	12	6	0.33	1.18	0.238	A	19	6	0.52	2.40	0.015	L
27♀	–	–	–	–	–	–	8	24	–0.50	2.65	0.007	R
28♀	11	16	–0.19	0.77	0.442	A	17	5	0.55	2.35	0.017	L
29♀	15	4	0.58	2.29	0.019	L	–	–	–	–	–	–
30♀	8	20	–0.43	2.08	0.036	R	–	–	–	–	–	–
31♀	18	4	0.64	2.77	0.004	L	16	3	0.68	2.75	0.004	L
32♀	–	–	–	–	–	–	19	8	0.41	2.31	0.019	L
33♀	–	–	–	–	–	–	14	1	0.87	3.10	0.001	L
34♀	–	–	–	–	–	–	7	11	–0.22	0.71	0.481	A
35♀	21	7	0.50	2.46	0.013	L	20	6	0.54	2.55	0.009	L
36♀	24	11	0.37	2.03	0.041	L	12	22	–0.29	1.54	0.121	A
37♀	10	9	0.05	0.00	1.000	A	–	–	–	–	–	–
38♀	–	–	–	–	–	–	17	4	0.62	2.62	0.007	L

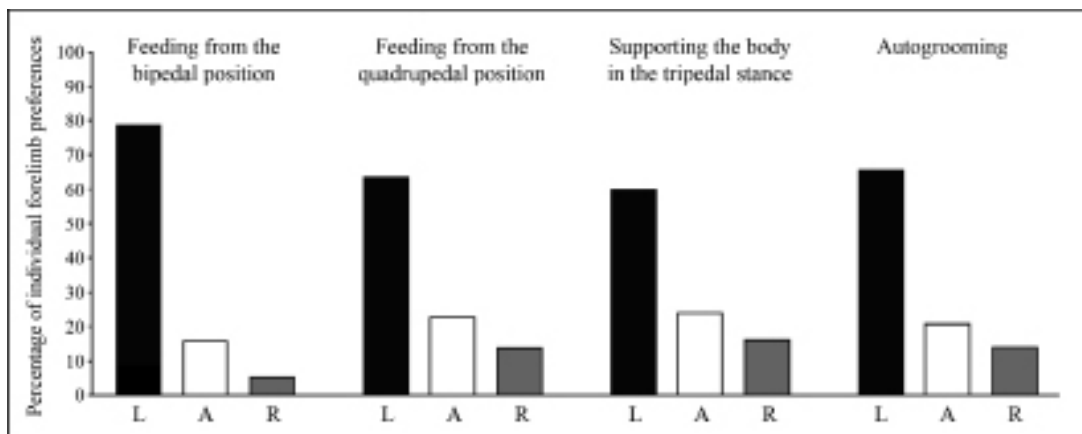


Fig. 23. Individual manual preferences in wild eastern grey kangaroos. Designations as in Fig. 9.

The left-forelimb preference for autogrooming was observed in 19 individuals (66%); the right-forelimb preference was observed in four individuals (14%); six individuals (20%) showed no preference (Fig. 23; Table 17). The number of lateralised individuals was considerably greater than that of non-lateralised ones (binomial test, $z = 2.97$, $p = 0.002$), and the number of left-handers exceeded considerably that of right-handers ($z = 2.92$, $p = 0.003$).

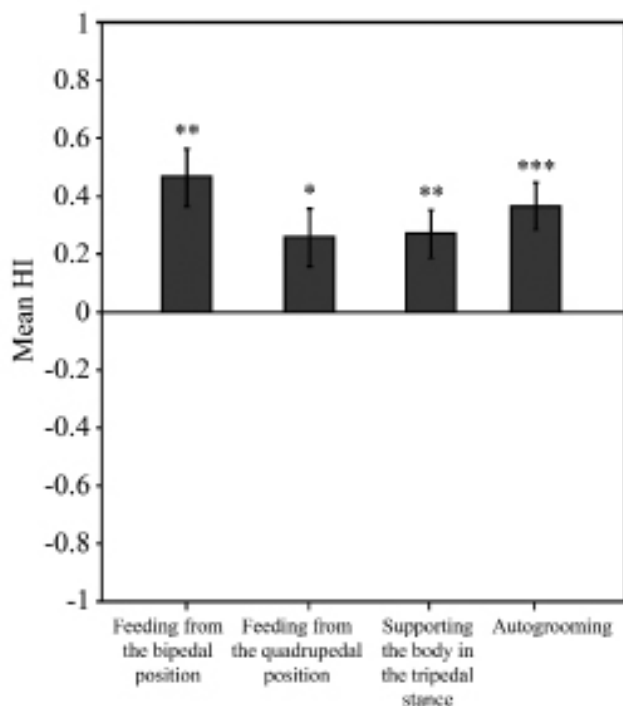


Fig. 24. Group-level laterality in wild eastern grey kangaroos. Designations as in Fig. 16.

A group-level preference of the left forelimb was found for all the behaviours: feeding from the bipedal position (mean HI \pm SEM = 0.47 ± 0.10 ; one-sample Wilcoxon signed-rank test, $W = 152$, $p = 0.001$, $n = 19$), feeding from the quadrupedal position (mean HI = 0.26 ± 0.10 ; $W = 138$, $p = 0.023$, $n = 22$), supporting the body in the tripedal stance (mean HI = 0.27 ± 0.08 ; $W = 192$, $p = 0.008$, $n = 25$) and autogrooming (mean HI = 0.37 ± 0.08 ; $W = 330$, $p < 0.001$, $n = 29$; Fig. 24).

3.5.2.3. Assessment of manual laterality by the route survey technique

In this analysis, we registered only one act of forelimb use for each behaviour from each individual encountered on the route. Comparison of the data obtained by route surveys revealed statistically significant differences between the two study sites at Maria Island (“Darlington” and “French's Farm”) for one of the behaviours, namely, for supporting the body in the tripedal stance ($z = 2.16$, $p = 0.031$, Z-test for proportions). For this reason, we did not pool the data for this behaviour. In “Darlington” area, the number of registered acts of the right forelimb use for supporting the body in the tripedal stance did not differ from that of registered acts of the left forelimb use (33 observations of the left forelimb use out of 64, binomial test $z = 1.63$, $p = 0.103$). At the same time, in “French's Farm” area most studied individuals showed the left-forelimb preference for supporting the body in the tripedal stance (41 observations of the left forelimb use out of 58, binomial test $z = 3.02$, $p = 0.002$).

The data on other behaviours did not differ between the study areas ($p > 0.05$, Z-test for proportions), and were pooled. The left-forelimb preference was found for feeding from the bipedal position (39 observations of the left forelimb use out of 48, binomial test, $z = 4.19$, $p < 0.001$), for feeding from the quadrupedal position (99 observations of the left forelimb use out of 135, $z = 1.00$, $p = 0.319$) and for autogrooming (47 observations of the left forelimb use out of 60, $z = 4.26$, $p < 0.001$).

3.6. Manual laterality in the brush-tailed bettong, *Bettongia penicillata*

3.6.1. Unimanual behaviours

Manual preferences in the brush-tailed bettong were studied for feeding on non-living food, catching live insects, supporting the body in the tripedal stance and manipulating nest material (Fig. 2). We obtained 31 act of forelimb use for taking non-living food (nuts, sliced fruit and vegetables) from each of the 15 studied individuals. For catching live insects, 36 acts of the use of one forelimb were obtained from each of the 13 individuals. To assess manual preferences for manipulating nest material, 29 acts of the use of one forelimb obtained from each of the 13 individuals were analysed. Brush-tailed bettongs used their paws only from the bipedal position when feeding on non-living food, catching live insects and manipulating nest material.

For the analysis of lateralised use of forelimbs for supporting the body in the tripedal stance, 44 acts of the use of one forelimb were obtained from each of the 14 individuals. In contrast to red-necked wallabies and eastern grey kangaroos, which assumed the tripedal

stance from the bipedal position, brush-tailed bettongs began to support the body in the tripod stance by raising one paw from the initial quadrupedal stance.

3.6.2. Distribution of individual preferences and group-level laterality in the use of forelimbs

The left-forelimb preference for feeding on non-living food was found in 13 individuals (86%), one individual (7%) preferred to use the right forelimb and one individual (7%) showed no preference (Fig. 25; Table 18). The number of lateralised individuals in the sample was considerably greater than that of non-lateralised ones (binomial test, $z = 3.10$, $p < 0.001$), and the number of left-handers exceeded considerably that of right-handers ($z = 2.94$, $p = 0.002$).

For catching live insects, 12 individuals (92%) showed the left-forelimb preference and one individual (8%) showed the right-forelimb preference (Fig. 25; Table 18). All 13 individuals were lateralised (binomial test, $z = 3.33$, $p < 0.001$), and the number of left-handers exceeded considerably that of right-handers ($z = 2.77$, $p = 0.003$).

Table 18.

Individual preferences in forelimb use for feeding in brush-tailed bettongs, *Bettongia penicillata* in captivity

Subject, sex	Feeding on non-living food						Catching of living insects					
	L	R	HI	z	p	Pref.	L	R	HI	z	p	Pref.
1♂	28	3	0.81	4.31	<0.001	L	33	3	0.83	4.83	<0.001	L
2♂	22	9	0.42	2.16	0.029	L	29	7	0.61	3.50	<0.001	L
3♂	24	7	0.55	2.87	0.003	L	27	9	0.50	2.83	0.004	L
4♂	26	5	0.68	3.59	<0.001	L	30	6	0.67	3.83	<0.001	L
5♂	22	9	0.42	2.16	0.029	L	31	5	0.72	4.17	<0.001	L
6♂	23	8	0.48	2.51	0.011	L	–	–	–	–	–	–
7♂	27	4	0.74	3.95	<0.001	L	–	–	–	–	–	–
8♂	20	11	0.29	1.44	0.150	A	26	10	0.44	2.50	0.011	L
9♂	27	4	0.74	3.95	<0.001	L	31	5	0.72	4.17	<0.001	L
10♀	25	6	0.61	3.23	<0.001	L	32	4	0.78	4.50	<0.001	L
11♀	29	2	0.87	4.67	<0.001	L	30	6	0.67	3.83	<0.001	L
12♀	8	23	-0.48	-2.51	0.011	R	10	26	-0.44	-2.50	0.011	R
13♀	27	4	0.74	3.95	<0.001	L	26	10	0.44	2.50	0.011	L
14♀	26	5	0.68	3.59	<0.001	L	33	3	0.83	4.83	<0.001	L
15♀	23	8	0.48	2.51	0.011	L	34	2	0.89	5.17	<0.001	L

The left-forelimb preference for supporting the body in the tripod stance was found in nine brush-tailed bettongs (64%); one individual (7%) preferred to support the body with the right forelimb; four individuals (29%) showed no preference (Fig. 25; Table 19). The number of lateralised individuals did not differ from that of non-lateralised ones (binomial test, $z = 1.34$, $p = 0.180$), but the number of left-handers among lateralised bettongs exceeded that of right-handers ($z = 2.21$, $p = 0.021$).

The left-forelimb preference for manipulating nest material was observed in 11 brush-tailed bettongs (84%); the right-forelimb preference was observed in one individual (8%);

Table 19.

Individual preferences in forelimb use for supporting of tripodal stance and nest material collecting in brush-tailed bettongs, *Bettongia penicillata* in captivity

Subject, sex	Supporting of tripodal stance						Nest material collecting					
	L	R	HI	z	p	Pref.	L	R	HI	z	p	Pref.
1♂	37	7	0.68	4.37	<0.001	L	25	4	0.72	3.71	<0.001	L
2♂	16	28	-0.27	-1.66	0.096	A	11	18	-0.24	-1.30	0.194	A
3♂	27	17	0.23	1.36	0.174	L	26	3	0.79	4.09	<0.001	L
4♂	30	14	0.36	2.26	0.023	L	27	2	0.86	4.46	<0.001	L
5♂	41	3	0.86	5.58	<0.001	L	23	6	0.59	2.97	0.002	L
6♂	27	17	0.23	1.36	0.174	A	-	-	-	-	-	-
7♂	38	6	0.73	4.67	<0.001	L	21	8	0.45	2.23	0.024	L
8♂	-	-	-	-	-	-	24	5	0.66	3.34	<0.001	L
9♂	40	4	0.82	5.28	<0.001	L	28	1	0.93	4.83	<0.001	L
10♀	24	20	0.09	0.45	0.652	A	25	4	0.72	3.71	<0.001	L
11♀	36	8	0.64	4.07	<0.001	L	26	3	0.79	4.09	<0.001	L
12♀	11	33	-0.50	-3.17	0.001	R	5	24	-0.66	-3.53	<0.001	R
13♀	39	5	0.77	4.97	<0.001	L	27	2	0.86	4.46	<0.001	L
14♀	37	7	0.68	4.37	<0.001	L	22	7	0.52	2.60	0.008	L
15♀	32	12	0.45	2.86	0.004	L	-	-	-	-	-	-

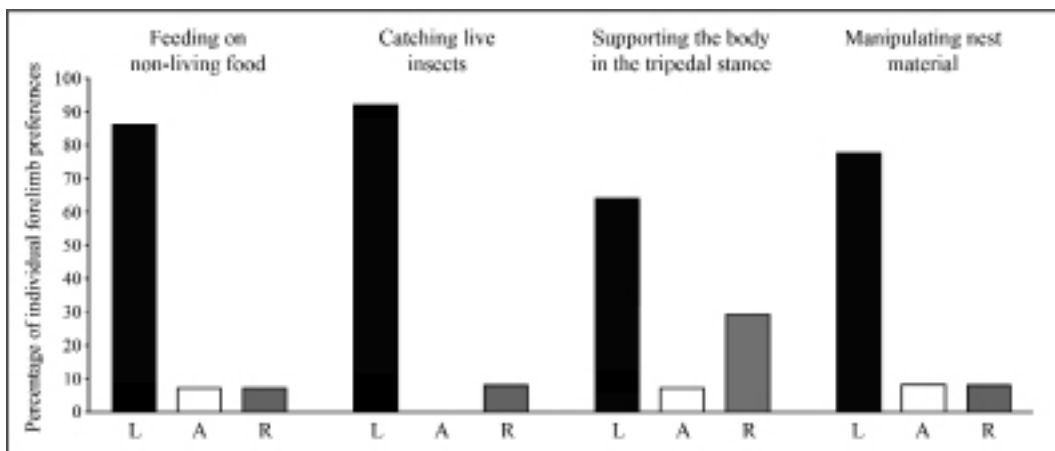


Fig. 25. Individual manual preferences in the brush-tailed bettong [Giljov et al., 2012d]. Designations as in Fig. 9.

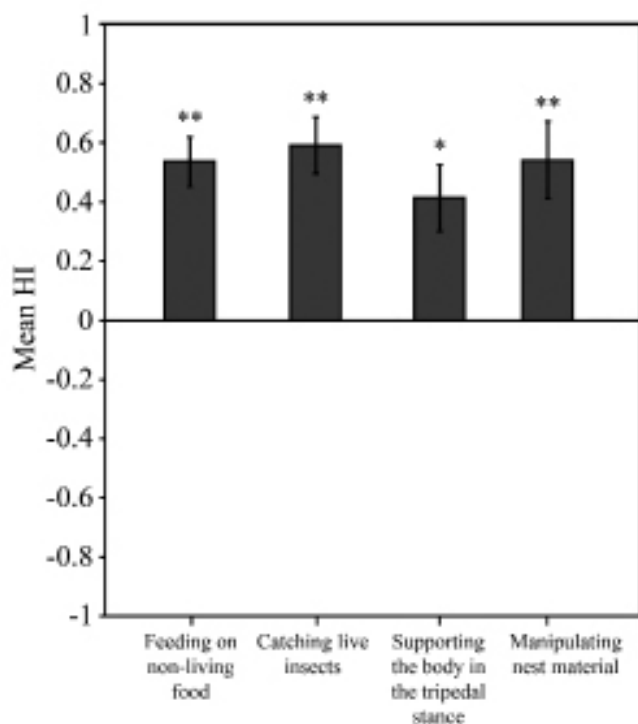


Fig. 26. Group-level laterality in the brush-tailed bettong [Giljov et al., 2012d]. Designations as in Fig. 16.

one other individual (8%) showed no preference (Fig. 25; Table 19). The number of lateralised individuals considerably exceeded that of non-lateralised ones (binomial test, $z = 2.77$, $p = 0.003$), and the number of left-handers among lateralised bettongs exceeded that of right-handers ($z = 2.60$, $p = 0.006$).

Brush-tailed bettongs showed a group-level preference of the left forelimb in all the four behaviours: feeding on non-living food (mean HI \pm SEM = 0.54 ± 0.08 ; one-sample Wilcoxon signed-rank test, $W = 112$, $p = 0.002$, $n = 15$), catching live insects (mean HI = 0.59 ± 0.10 ; $W = 87$, $p = 0.003$, $n = 13$), supporting the body in the tripodal stance (mean HI = 0.41 ± 0.11 ; $W = 83$, $p = 0.010$, $n = 14$) and manipulating nest material (mean HI = 0.54 ± 0.13 ; $W = 79$, $p = 0.006$, $n = 13$; Fig. 26).

3.7. Manual laterality in the red kangaroo, *Macropus (Osphranter) rufus*

3.7.1. Unimanual behaviours

Manual preferences of red kangaroos were studied for feeding from the bipedal position, feeding from the quadrupedal position, supporting the body in the tripodal stance and autogrooming [Giljov et al., 2015a]. To assess manual preferences for feeding from the bipedal position, on the average 21 act of the use of one forelimb per individual were obtained

for 21 individuals (15–33 acts from an individual). To assess manual preferences for feeding from the quadrupedal position, on the average 23 acts per individual were obtained for 28 individuals (15–41 acts from an individual).

Similarly to red-necked wallabies and eastern grey kangaroos, red kangaroos began supporting the body in the tripedal stance by lowering one paw from the bipedal position. Manual preferences for supporting the body in the tripedal stance were assessed on the basis of 20 acts of the use of one forelimb per individual (on the average) obtained for 16 individuals (15–26 acts from an individual). For the analysis of manual preferences for autogrooming, on the average 21 act of the use of one forelimb for snout cleaning from the bipedal position per individual was obtained for 20 individuals (15–32 acts from an individual).

3.7.2. Distribution of individual and group-level manual preferences

The left-forelimb preference for feeding from the bipedal position was found in 18 individuals (86%); the right-forelimb preference was found in one individual (5%); two individuals (9%) showed no preference (Fig. 27; Table 20). The number of lateralised individuals exceeded considerably that of non-lateralised ones (binomial test, $z = 3.49$, $p < 0.001$), and the number of left-handers was significantly greater than that of right-handers ($z = 3.67$, $p < 0.001$).

The left-forelimb preference for feeding from the quadrupedal position was found in 20 individuals (72%); the right limb forelimb preference was found in four individuals (14%); four other individuals (14%) showed no preference (Fig. 27; Table 20). The number of lateralised individuals was considerably greater than that of non-lateralised ones (binomial test, $z = 3.59$, $p < 0.001$), and the number of left-handers was considerably greater than number of right-handers ($z = 3.06$, $p = 0.002$).

The left-forelimb preference for supporting the body in the tripedal stance was found in 12 red kangaroos (74%); the right-forelimb preference was found in two individuals (13%); two

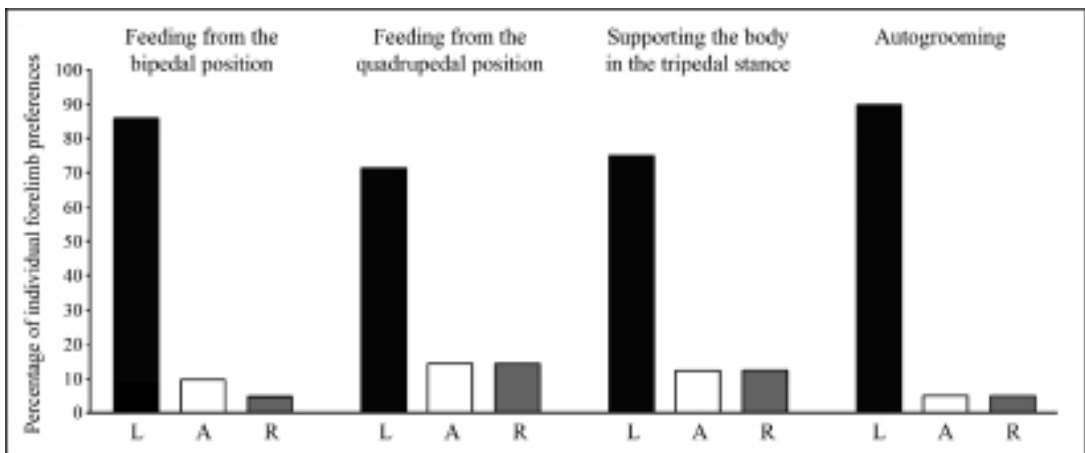


Fig. 27. Individual manual preferences of wild red kangaroos. Designations as in Fig. 9.

Table 20.

Individual preferences in forelimb use for feeding in red kangaroo,
Macropus (Osphranter) rufus in the wild

Subject, sex	Feeding from the bipedal position						Feeding from the quadrupedal position					
	L	R	HI	z	p	Pref.	L	R	HI	z	p	Pref.
1♂	17	3	0.70	2.91	0.003	L	18	6	0.50	2.25	0.023	L
2♂	–	–	–	–	–	–	23	8	0.48	2.51	0.011	L
3♂	17	10	0.26	1.15	0.248	A	2	15	–0.76	–2.91	0.002	R
4♂	19	0	1.00	4.13	<0.001	L	–	–	–	–	–	–
5♂	13	3	0.63	2.25	0.021	L	15	3	0.67	2.59	0.008	L
6♂	–	–	–	–	–	–	12	8	0.20	0.67	0.503	A
7♂	–	–	–	–	–	–	–	–	–	–	–	–
8♂	21	3	0.75	3.47	<0.001	L	–	–	–	–	–	–
9♂	–	–	–	–	–	–	24	7	0.55	2.87	0.003	L
10♂	–	–	–	–	–	–	20	5	0.60	2.80	0.004	L
11♂	18	4	0.64	2.77	0.004	L	16	4	0.60	2.46	0.012	L
12♂	–	–	–	–	–	–	–	–	–	–	–	–
13♂	–	–	–	–	–	–	15	0	1.00	3.61	<0.001	L
14♂	–	–	–	–	–	–	28	9	0.51	2.96	0.003	L
15♂	–	–	–	–	–	–	14	3	0.65	2.43	0.013	L
16♀	2	16	–0.78	3.06	0.001	R	–	–	–	–	–	–
17♀	–	–	–	–	–	–	19	5	0.58	2.65	0.007	L
18♀	–	–	–	–	–	–	25	8	0.52	2.79	0.005	R
19♀	13	3	0.63	2.25	0.021	L	18	1	0.89	3.67	<0.001	L
20♀	18	6	0.50	2.25	0.023	L	–	–	–	–	–	–
21♀	10	8	0.11	0.24	0.815	A	12	7	0.26	0.92	0.359	A
22♀	16	0	1.00	3.75	<0.001	L	24	2	0.85	4.12	<0.001	L
23♀	–	–	–	–	–	–	–	–	–	–	–	–
24♀	28	4	0.75	4.07	<0.001	L	–	–	–	–	–	–
25♀	–	–	–	–	–	–	19	0	1.00	4.13	<0.001	L
26♀	26	7	0.58	3.13	0.001	L	17	5	0.55	2.35	0.017	L
27♀	15	3	0.67	2.59	0.008	L	22	14	0.22	1.17	0.243	A
28♀	15	0	1.00	3.61	<0.001	L	–	–	–	–	–	–
29♀	20	7	0.48	2.31	0.019	L	0	15	–1.00	–3.61	<0.001	R
30♀	–	–	–	–	–	–	18	6	0.50	2.25	0.023	L
31♀	19	6	0.52	2.40	0.015	L	16	3	0.68	2.75	0.004	L
32♀	–	–	–	–	–	–	17	1	0.89	3.54	<0.001	L
33♀	15	4	0.58	2.29	0.019	L	–	–	–	–	–	–
34♀	13	2	0.73	2.58	0.007	L	–	–	–	–	–	–
35♀	–	–	–	–	–	–	5	17	–0.55	–2.35	0.017	R
36♀	–	–	–	–	–	–	–	–	–	–	–	–
37♀	27	5	0.69	3.71	<0.001	L	32	9	0.56	3.44	<0.001	L
38♀	–	–	–	–	–	–	18	5	0.57	2.50	0.011	L
39♀	–	–	–	–	–	–	–	–	–	–	–	–
40♀	–	–	–	–	–	–	12	5	0.41	1.46	0.143	A
41♀	12	3	0.60	2.07	0.035	L	18	0	1.00	4.01	<0.001	L

Table 21.

Individual preferences of forelimb use for supporting of tripedal stance and autogrooming in red kangaroo, *Macropus (Osphranter) rufus* in the wild

Subject, sex	Supporting of tripedal stance						Autogrooming					
	L	R	HI	z	p	Pref.	L	R	HI	z	p	Pref.
1♂	–	–	–	–	–	–	–	–	–	–	–	–
2♂	17	3	0.70	2.91	0.003	L	–	–	–	–	–	–
3♂	–	–	–	–	–	–	10	6	0.25	0.75	0.454	A
4♂	14	2	0.75	2.75	0.004	L	17	3	0.70	2.91	0.003	L
5♂	–	–	–	–	–	–	–	–	–	–	–	–
6♂	–	–	–	–	–	–	–	–	–	–	–	–
7♂	19	3	0.73	3.20	<0.001	L	14	3	0.65	2.43	0.013	L
8♂	16	5	0.52	2.18	0.027	L	21	4	0.68	3.20	<0.001	L
9♂	–	–	–	–	–	–	16	0	1.00	3.75	<0.001	L
10♂	–	–	–	–	–	–	–	–	–	–	–	–
11♂	14	2	0.75	2.75	0.004	L	–	–	–	–	–	–
12♂	–	–	–	–	–	–	16	3	0.68	2.75	0.004	L
13♂	4	21	–0.68	–3.20	<0.001	R	–	–	–	–	–	–
14♂	23	1	0.92	4.29	<0.001	L	23	1	0.92	4.29	<0.001	L
15♂	–	–	–	–	–	–	–	–	–	–	–	–
16♀	–	–	–	–	–	–	–	–	–	–	–	–
17♀	19	4	0.65	2.92	0.003	L	22	8	0.47	2.37	0.016	L
18♀	–	–	–	–	–	–	–	–	–	–	–	–
19♀	14	3	0.65	2.43	0.013	L	–	–	–	–	–	–
20♀	–	–	–	–	–	–	13	2	0.73	2.58	0.007	L
21♀	–	–	–	–	–	–	17	1	0.89	3.54	<0.001	L
22♀	–	–	–	–	–	–	–	–	–	–	–	–
23♀	7	11	–0.22	–0.71	0.481	A	24	8	0.50	2.65	0.007	L
24♀	20	6	0.54	2.55	0.009	L	25	0	1.00	4.80	<0.001	L
25♀	–	–	–	–	–	–	–	–	–	–	–	–
26♀	–	–	–	–	–	–	–	–	–	–	–	–
27♀	13	8	0.24	0.87	0.383	A	–	–	–	–	–	–
28♀	–	–	–	–	–	–	14	3	0.65	2.43	0.013	L
29♀	–	–	–	–	–	–	–	–	–	–	–	–
30♀	14	3	0.65	2.43	0.013	L	25	2	0.85	4.23	<0.001	L
31♀	21	5	0.62	2.94	0.002	L	17	6	0.48	2.09	0.035	L
32♀	–	–	–	–	–	–	20	6	0.54	2.55	0.010	L
33♀	–	–	–	–	–	–	–	–	–	–	–	–
34♀	16	0	1.00	3.75	<0.001	L	18	5	0.57	2.50	0.011	L
35♀	2	13	–0.73	–2.58	0.007	R	–	–	–	–	–	–
36♀	–	–	–	–	–	–	17	4	0.62	2.62	0.007	L
37♀	–	–	–	–	–	–	–	–	–	–	–	–
38♀	–	–	–	–	–	–	–	–	–	–	–	–
39♀	–	–	–	–	–	–	2	14	–0.75	–2.75	0.004	R
40♀	–	–	–	–	–	–	–	–	–	–	–	–
41♀	–	–	–	–	–	–	16	3	0.68	2.91	<0.001	L

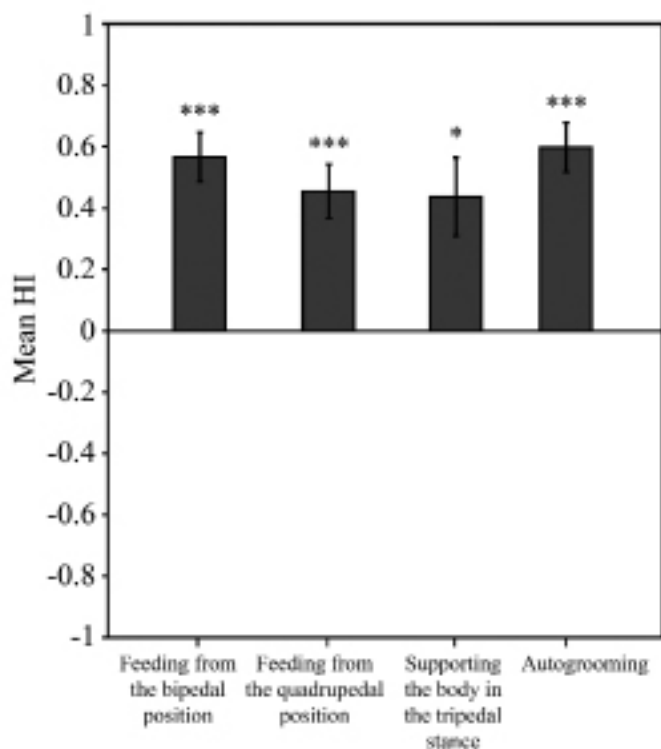


Fig. 28. Group-level laterality in wild red kangaroos. Designations as in Fig. 10; * $p < 0.05$; *** $p < 0.001$.

other individuals (13%) showed no preference (Fig. 27; Table 21). The number of lateralised individuals was significantly greater than that of non-lateralised ones (binomial test, $z = 2.75$, $p = 0.004$), and the number of left-handers exceeded that of right-handers ($z = 2.41$, $p = 0.013$).

The left-forelimb preference for autogrooming was observed in 18 red kangaroos (90%); the right-forelimb preference was observed in one individual (5%); one other individual (5%) showed no preference (Fig. 27; Table 21). The number of lateralised individuals was considerably greater than that of non-lateralised ones (binomial test, $z = 3.80$, $p < 0.001$), and the number of left-handers exceeded that of right-handers ($z = 3.67$, $p < 0.001$).

Red kangaroos showed a group-level preference of the left forelimb in all the four behaviours: feeding from the bipedal position (mean HI \pm SEM = 0.57 ± 0.08 ; one-sample Wilcoxon signed-rank test, $W = 195$, $p < 0.001$, $n = 21$), feeding from the quadrupedal position (mean HI = 0.46 ± 0.09 ; $W = 289$, $p < 0.001$, $n = 28$), supporting the body in the tripodal stance (mean HI = 0.44 ± 0.13 ; $W = 93$, $p = 0.014$, $n = 16$) and autogrooming (mean HI = 0.61 ± 0.08 ; $W = 180$, $p < 0.001$, $n = 20$; Fig. 28).

3.8. Conclusion

We studied manual laterality in seven species of marsupials. In each species manual laterality for at least four unimanual behaviours was studied. Manual preferences in the grey short-tailed opossum (Didelphidae), the sugar glider (Petauridae) and the brush-tailed bet-

tong (Potoroidae) was assessed for the following behaviours: manipulating non-living food objects, catching live prey, supporting the body in the tripod stance and manipulating nest material. In the Goodfellow's tree kangaroo, the red-necked wallaby, the eastern grey kangaroo and the red kangaroo (Macropodidae) manual preferences was studied for manipulating food from the bipedal and from the quadrupedal position, for autogrooming and for supporting the body in the tripod stance. Our results demonstrated the presence of individual manual preferences in all the species under study. The proportion of left-handers, right-handers and non-lateralised individuals varied between species. Group-level laterality in the use of forelimbs was found in four species: the red-necked wallaby, the eastern grey kangaroo, the red kangaroo and the brush-tailed bettong. In the other three species no laterality at the group level was observed.

The analysis of the data obtained by the route surveys during night observations revealed the same trends in the manual laterality as the analysis of the data obtained during continuous daytime observations both in the red-necked wallaby and the eastern grey kangaroo. The route survey technique did not allow us to assess individual preferences but did allow taking into account considerably more individuals for the assessment of the group-level laterality than continuous observations on separate groups of animals. The fact that we obtained similar results with the use of two different methods of data collection lends additional support to the trends found in the study.

Manual laterality has been studied in many vertebrate species [Ströckens et al., 2013]. Among placentals (Placentalia), hand preferences have been studied systematically and comprehensively in primates (Primates) [Hook, 2004; Meguerditchian et al., 2012]. Almost all studied primate species show individual left- or right-hand preferences but only a few of them display laterality at the group level [Ströckens et al., 2013]. Our results indicate that manual laterality in marsupials is in general comparable with that in primates. In both taxa it can be expressed at the individual as well as the group level, and the expression may vary depending on the species, the sex of the animal, and the characteristics of the actions.

Besides the seven species studied in this work and previously [grey short-tailed opossums: Ivanco et al., 1996; red-necked wallabies: Spiezio et al., 2016], three other marsupials have been investigated in this respect. Brush-tailed possums, *Trichosurus vulpecula* (Phalangeridae) showed individual forelimb preferences in the experiment, securing a food reward from a narrow feeding tube [Megirian et al., 1977]. In the stripe-faced dunnart, *Sminthopsis macroura* (Dasyuridae) lateralised perception of visual information was recorded [Lippolis et al., 2005]. Auditory laterality was found in the southern hairy-nosed wombat, *Lasiornhinus latifrons* (Vombatidae) [Descovich et al., 2013]. Altogether, manual laterality has been studied in the representatives of three orders (Didelphimorphia, Diprotodontia, Dasyuromorphia) and five families (Didelphidae, Petauridae, Phalangeridae, Potoroidae, Macropodidae) of marsupials. The results of studies on marsupials lend further support to the opinion that manual preferences and behavioural lateralisation in general are widespread in mammals [Rogers, 2002; Hook, 2004; Vallortigara et al., 2011; Ströckens et al., 2013].

THE EFFECT OF CHARACTERISTICS OF ACTIONS ON MANUAL LATERALITY IN MARSUPIALS

Characteristics of a unimanual action may have a significant effect on the manifestation of laterality (see section 1.3). Taking this into account, we compared the within species manual preferences across different behaviours. Two measures are commonly used to assess how various factors affect manual laterality: (1) direction, reflecting the left- or the right-hand bias in laterality, and (2) degree, reflecting the strength of the lateral bias regardless of its direction [Rogers, 2002; Wells, 2003; Hopkins et al., 2011; Meguerditchian et al., 2012]. The values of the handedness index (HI) are used to reveal the effect of a factor on the direction of laterality. To assess the influence of a factor on the strength of lateralisation, the absolute handedness index (Abs-HI) is used, that is, the values of HI irrespective of the plus/minus sign [Westergaard et al., 1998; Wells, 2003; Braccini et al., 2010; Hopkins et al., 2011; Meguerditchian et al., 2012]. The effect of the behaviour on the manifestations of manual preferences in marsupials was assessed using Friedman test and Bonferroni–Dunn post hoc test [Dunn, 1961] for the subsequent pairwise comparison of the behaviours. Multiple comparisons with the use of Bonferroni–Dunn test are widely used in studies of behavioural lateralisation [Gagliardo, et al., 2001; Domenici et al., 2012; Cormier, Tremblay, 2013].

4.1. The effect of the behaviour on manual laterality in quadrupedal marsupials

No effect of the behaviour on the expression of manual laterality was found in the studied quadrupedal species of marsupials: the grey short-tailed opossum, the sugar glider and the Goodfellow’s tree kangaroo [Giljov et al., 2012a, 2013]. The analysis of the effect of this factor in each of these species is given below.

The type of unimanual behaviour of grey short-tailed opossums did not influence the direction of preferences either in males (Friedman test, $\chi^2_{(3)} = 6.90$, $p = 0.075$) or in females ($\chi^2_{(3)} = 0.28$, $p = 0.964$). Pairwise comparison of the behaviours did not reveal any significant difference in the direction of lateralised forelimb use in both sexes, either ($p > 0.05$, Bonferroni–Dunn test). The strength of manual laterality did not differ significantly across the studied behaviours (Friedman test, $\chi^2_{(3)} = 4.11$, $p = 0.250$). No significant differences in the degree of motor laterality were found during the subsequent pairwise comparison of the behaviours, either ($p > 0.05$, Bonferroni–Dunn test).

In the sugar glider, the unimanual behaviour did not influence the direction of motor preferences either in males (Friedman test, $\chi^2_{(3)} = 1.93$, $p = 0.586$) or in females ($\chi^2_{(3)} = 4.44$, $p = 0.218$). No significant differences in the direction of lateralisation were found after pairwise comparison of the behaviours in both sexes, either ($p > 0.05$, Bonferroni–Dunn test). No significant differences in the strength of lateralisation between the studied behaviours were revealed (Friedman test, $\chi^2_{(3)} = 4.20$, $p = 0.241$). No significant differences were found after the subsequent pairwise comparison of the behaviours, either ($p > 0.05$, Bonferroni–Dunn test).

We did not find any effect of the type of behaviour on the direction of lateralisation in the use of forelimbs in Goodfellow’s tree kangaroo (Friedman test, $\chi^2_{(3)} = 2.31$, $p = 0.510$). Subsequent pairwise comparison of the behaviours also showed the absence of any statistically significant differences in the direction of lateralisation ($p > 0.05$, Bonferroni–Dunn test). No significant differences in the strength of lateralisation were found between the studied behaviours (Friedman test $\chi^2_{(3)} = 0.86$, $p = 0.836$). We failed to reveal any differences in the degree of lateralisation by subsequent pairwise comparison of the behaviours ($p > 0.05$, Bonferroni–Dunn test).

4.2. The effect of the behaviour on manual laterality in bipedal marsupials

4.2.1. The red-necked wallaby, *Macropus (Notamacropus) rufogriseus*

In captive red-necked wallabies, a significant effect of the behaviour on the direction of manual preferences was found (Friedman test, $\chi^2_{(3)} = 30.52$, $p < 0.001$). Subsequent pairwise comparison of the behaviours revealed the presence of statistically significant differences in the direction of lateralisation between feeding from the bipedal position and feeding from the quadrupedal position, between feeding from the bipedal position and supporting the body in the tripodal stance, between autogrooming and feeding from the quadrupedal position as well as between autogrooming and supporting the body in the tripodal stance ($p < 0.05$, Bonferroni–Dunn test). The direction of lateralisation did not differ significantly between feeding from the quadrupedal position and supporting the body in the tripodal stance or between autogrooming and feeding from the bipedal position ($p > 0.05$, Bonferroni–Dunn test).

Comparison of the strength of laterality in various behaviours in the red-necked wallaby showed that manual preferences were stronger for autogrooming than for supporting the body in the tripodal stance (Wilcoxon matched-pairs signed rank test, $W = 53$, $p = 0.004$, $n_1 = n_2 = 10$). No other differences between the behaviours were found ($p > 0.05$, Wilcoxon matched-pairs signed rank test).

In wild wallabies the direction of manual laterality was influenced by the unimanual behaviour. Significant differences in the direction of lateralisation were found between feeding from the bipedal position and feeding from the quadrupedal position (Wilcoxon matched-pairs signed rank test, $W = -59$, $p = 0.040$; $n_1 = n_2 = 13$), between feeding from the bipedal position and supporting the body in the tripodal stance ($W = -108$, $p < 0.001$; $n_1 = n_2 = 15$), between feeding from the quadrupedal position and supporting the body in the tripodal stance ($W = -56$, $p = 0.027$; $n_1 = n_2 = 12$), between autogrooming and feeding from the quadrupedal position ($W = 11$, $p = 0.007$; $n_1 = n_2 = 11$), as well as between autogrooming and supporting the body in the tripodal stance ($W = 10$, $p = 0.002$; $n_1 = n_2 = 10$). The direction of laterality for feeding from the bipedal position and for autogrooming did not differ

significantly (Wilcoxon matched-pairs signed rank test, $W = 48$, $p = 0.064$; $n_1 = n_2 = 13$). Type of behaviour also had a significant effect on the strength of laterality (Friedman test, $\chi^2_{(3)} = 18.30$, $p < 0.001$). After pairwise comparison, the strength of laterality was found to be higher for feeding from the bipedal position and supporting the body in the tripodal stance than for feeding from the quadrupedal position ($p < 0.05$, Bonferroni–Dunn test). Manual preferences for autogrooming were expressed more strongly than for feeding from the quadrupedal position ($p < 0.05$, Bonferroni–Dunn test). No significant differences, in contrast, were found between feeding from the bipedal position and supporting the body in the tripodal stance, between autogrooming and feeding from the bipedal position or between autogrooming and supporting the body in the tripodal stance ($p > 0.05$, Bonferroni–Dunn test).

4.2.2. The eastern grey kangaroo, *Macropus (Macropus) giganteus*

In captive eastern grey kangaroos, the behaviour had an effect on the direction of manual preferences (Friedman test, $\chi^2_{(3)} = 13.96$, $p = 0.003$). Pairwise comparison of the behaviours revealed statistically significant differences in the direction of laterality between feeding from the bipedal position and feeding from the quadrupedal position, as well as between autogrooming and feeding from the quadrupedal position ($p < 0.05$, Bonferroni–Dunn test). The direction of lateralisation did not differ significantly between the other behaviours ($p > 0.05$, Bonferroni–Dunn test). Significant differences in the strength of laterality between the behaviours were found (Friedman test, $\chi^2_{(3)} = 18.36$, $p < 0.001$). Manual preferences for feeding from the bipedal position and for autogrooming were stronger than for feeding from the quadrupedal position ($p < 0.05$, Bonferroni–Dunn test). The strength of laterality did not differ significantly between the other behaviours ($p > 0.05$, Bonferroni–Dunn test).

In wild eastern grey kangaroos, the unimanual behaviour also influenced the direction of motor preferences. Statistically significant differences were found between feeding from the bipedal position and feeding from the quadrupedal position (Wilcoxon matched-pairs signed rank test, $W = -41$, $p = 0.037$; $n_1 = n_2 = 10$), between feeding from the bipedal position and supporting the body in the tripodal stance ($W = -62$, $p = 0.012$; $n_1 = n_2 = 12$), between feeding from the quadrupedal position and autogrooming ($W = 118$, $p = 0.012$; $n_1 = n_2 = 19$) as well as between autogrooming and supporting the body in the tripodal stance ($W = 86$, $p = 0.025$; $n_1 = n_2 = 16$). No significant differences between feeding from the bipedal position and autogrooming or between feeding from the quadrupedal position and supporting the body in the tripodal stance were found ($p > 0.05$, Wilcoxon signed-rank test). No statistically significant differences in the degree of laterality between the studied behaviours were found ($p > 0.05$, Wilcoxon matched-pairs signed rank test).

4.2.3. The brush-tailed bettong, *Bettongia penicillata*

In brush-tailed bettongs, the unimanual behaviour did not influence the direction of motor preferences (Friedman test, $\chi^2_{(3)} = 3.33$, $p = 0.344$) [Giljov et al., 2012d]. No statistically significant differences in the direction of lateralisation were found after pairwise comparison of the behaviours, either ($p > 0.05$, Bonferroni–Dunn test). There were no significant differences in the strength of laterality between the studied behaviours (Friedman test, $\chi^2_{(3)} = 2.24$, $p = 0.525$). Pairwise comparison of the behaviours did not reveal any differences in the strength of laterality, either ($p > 0.05$, Bonferroni–Dunn test).

4.2.4. The red kangaroo, *Macropus (Osphranter) rufus*

In red kangaroos, the unimanual behaviour did not influence the direction of manual laterality ($p > 0.05$, Wilcoxon matched-pairs signed rank test). The degree of manual laterality did not differ significantly between the studied behaviours ($p > 0.05$, Wilcoxon signed-rank test).

4.3. Conclusion

We found no differences in the expression of manual laterality for different unimanual behaviours in the grey short-tailed opossum, the sugar glider, the Goodfellow's tree kangaroo, the red kangaroo and the brush-tailed bettong. It is especially interesting that there were no differences in manual preferences for feeding on non-living food and for catching live insects in the grey short-tailed opossum, the sugar glider and the brush-tailed bettong. According to the classification of unimanual tasks in primates [Fagot, Vauclair, 1991], feeding on static food objects that do not have to be processed is a low-level task, while catching of live prey is a high-level task requiring speed and precision. In primates high-level tasks elicit stronger manual lateralisation than low-level tasks [Fagot, Vauclair, 1991; King, Landau, 1993; Westergaard, Suomi, 1996]. However, in grey short-tailed opossums, sugar gliders and brush-tailed bettongs no differences either in the direction or in the strength of manual preferences were found between actions differing in complexity. In contrast to placentals studied in this respect, manual laterality in marsupials does not depend on the complexity of the task (low-level vs. high-level task).

In contrast to the above species, in the red-necked wallaby the behaviour did have a significant effect on the manifestations of laterality. Feeding from the quadrupedal position was the only behaviour in which the number of left-handers did not differ significantly from that of right-handers and no group-level laterality was found. Incidentally, this was also the only behaviour considered in our study in which wallabies initially (that is, before the unimanual action) stood on all four limbs. Our results indicate that in the red-necked wallaby individual and group-level laterality is more strongly expressed in actions performed from the bipedal position as compared to actions performed from the quadrupedal position. A similar trend has been recorded in primates. Stronger lateralisation at the individual and/or group level associated with the performance of actions from the bipedal position as compared to the quadrupedal position has been observed in most primate species studied in this respect [Hopkins, 1993; Ward et al., 1993; Westergaard et al., 1997, 1998; Blois-Heulin et al., 2007; Braccini et al., 2010].

The reasons why the body posture should influence the manifestations of laterality in primates are unstudied. It is thought that instability of the bipedal posture results in the excitation of the nervous system and a stronger motor laterality [Ward, 1995]. Wallabies are adapted well to bipedal locomotion and can support bipedal body posture easily [Hume et al., 1989]. It is unlikely that the stronger laterality in the bipedal posture is due to its instability. In terrestrial macropods (Macropodidae), the assumption of the bipedal posture is associated with antipredator vigilance [Blumstein, Daniel, 2003; Nielsen, 2009]. A kangaroo in an upright position has a better view of the surroundings than a kangaroo in the quadrupedal or recumbent position, which are common during feeding and resting (in both positions the body is horizontally orientated), and can start fast bipedal locomotion almost at once. It has been shown that the activation of the nervous system (for instance, in an activity involving

greater vigilance) may result in a more pronounced behavioural lateralisation in animals [Fagot, Vauclair, 1991]. We may suggest that the association between the bipedal posture and the state of greater vigilance may determine stronger manual preferences of the red-necked wallaby in the bipedal position as compared to the quadrupedal position. The mechanism of the body posture effect on laterality either in placentals or in marsupials apparently calls for further research.

In the eastern grey kangaroo, the expression of the left-forelimb preference for feeding and autogrooming (performed from the bipedal position) was stronger than for feeding from the quadrupedal position. However the influence of body posture on laterality is weaker than in the red-necked wallaby. Possible causes of a weak or non-existent postural effect in all the studied species except the red-necked wallaby are discussed in Chapter 7.

In the red-necked wallaby, the direction of manual preferences for supporting the body in the tripodal stance was different from that for manipulating food from the bipedal position and for autogrooming. In all the three behaviours the forelimb was chosen in the bipedal position (to remind, wallabies assume the tripodal stance from the bipedal position putting forward a forelimb and leaning on it). This means that the body posture during the unimanual action could not be the reason of the differences between the behaviours. However, these differences might be explained by the forelimb function in various behaviours. According to the postural origins theory of handedness, arboreal primates evolved manual laterality because of the need to simultaneously manipulate food and support the body in an unstable position on tree branches [MacNeilage, 1991, 2007]. Manual specialisation was found in some arboreal species of primates: the left hand is used for feeding and the right hand, for support [Ward, 1995; Milliken et al., 2005; Rigamonti et al., 2005]. A similar division of functions between the forelimbs in actions performed from the bipedal position is observed in the red-necked wallaby even though it is a terrestrial species. At the same time, no differences between forelimb preferences for manipulations and for supporting the body were found in Goodfellow's tree kangaroo, which lives on trees. Apparently the postural origins theory of handedness is inapplicable to the studied marsupials because in the latter the division of functions between the left and the right forepaw is not associated with the arboreal way of life.

In two other terrestrial macropods, the eastern grey kangaroo and the red kangaroo, the direction of laterality was the same for supporting the body and for manipulations, that is, no functional specialisation of the paws was observed. Differences between these two kangaroo species and the red-necked wallaby may be explained by the character of feeding. While eastern grey kangaroos and red kangaroos feed on low-growing plants, a considerable part of the diet of red-necked wallabies is represented by leaves of trees and shrubs [Frith, Calaby, 1969; Tyndale-Biscoe, 2005; Dawson, 2012]. For feeding on tall plants, the wallabies need both forepaws. As shown in this study, when feeding bimanually red-necked wallabies used in most instances the right forepaw to support the branch of a tree or a shrub at the necessary height, manipulating leaves and shoots and directing them to the mouth with the left forepaw. This means that both in the unimanual and in the bimanual activity red-necked wallabies preferred to use the right paw for actions associated with static effort and the left paw for actions involving finer coordination. A similar division of manual functions has been found in Bonnet macaques, *Macaca radiata*. The hand preferentially use for support is also preferred for other physically demanding actions (e.g., for climbing trees), whereas the hand preferred for feeding is preferentially employed for other fine manipulative tasks such as autogrooming [Mangalam et al., 2014]. Different directions of laterality in functionally different unimanual

behaviours (body support and manipulations during feeding/autogrooming) might have evolved in the red-necked wallaby precisely because of the necessity for the division of functions between forelimbs in bimanual actions. By the same token, the same direction of laterality in all unimanual actions in the eastern grey kangaroo and the red kangaroo might be due to the fact that they feed on low vegetation and so do not need to use both forepaws simultaneously for various tasks.

THE EFFECT OF SEX AND AGE ON MANUAL LATERALITY IN MARSUPIALS

To assess the effect of sex and age on the manual preferences, we used two measures: direction and strength of laterality [Giljov et al., 2013, 2015a]. Sex differences in the expression of laterality were assessed using a Mann-Whitney U test [Mann, Whitney, 1947]. To assess the correlation between the forelimb preference and the age of individuals, Spearman rank-order correlation was used [Caruso, Cliff, 1997]. This analysis was conducted for the grey short-tailed opossum, the sugar glider and the Goodfellow's tree kangaroo. In the case of red-necked wallaby and the eastern grey kangaroo, the information about the exact age of the individuals was lacking and the types of unimanual behaviours were different in the adults and the young. For these reasons, manual preferences in these two species was analysed separately in three age classes: adults, young-at-foot, and pouch young. No data on the age of brush-tailed bettongs and red kangaroos were available.

5.1. The effect of sex and age on manual laterality in quadrupedal marsupials

5.1.1. Grey short-tailed opossum, *Monodelphis domestica*

In grey short-tailed opossums significant sex differences in the direction of manual preferences were found in all the behaviours: feeding on non-living food (Mann-Whitney U test, $U = 28.0$, $p = 0.004$), feeding on insects ($U = 20.0$, $p = 0.001$), supporting the body in the tripedal stance ($U = 18.0$, $p < 0.001$) and manipulating nest material ($U = 32.5$, $p = 0.009$). Therefore, the data on males and females were analysed separately in subsequent analyses.

Males of the grey short-tailed opossum showed the right-forelimb preference for three behaviours: feeding on non-living food (mean HI \pm SEM = -0.21 ± 0.08 ; one-sample Wilcoxon signed-rank test, $W = -53$, $p = 0.041$, $n = 12$), feeding on insects (mean HI = -0.32 ± 0.10 ; $W = -61$, $p = 0.018$, $n = 12$) and supporting the body in the tripedal stance (mean HI = -0.33 ± 0.09 ; $W = -66$, $p = 0.011$, $n = 12$). Male grey short-tailed opossums as a subgroup did not show any statistically significant manual preference for manipulating nest material (mean HI = -0.22 ± 0.13 ; $W = -42$, $p = 0.107$, $n = 12$).

Females of the grey short-tailed opossum showed the left-forelimb preference in all the behaviours: feeding on non-living food (mean HI \pm SEM = 0.23 ± 0.08 ; one-sample Wilcoxon signed-rank test, $W = 66$, $p = 0.041$, $n = 14$), feeding on insects (mean HI = 0.32 ± 0.10 ; $W = 78$, $p = 0.016$, $n = 14$), manipulating nest material (mean HI = 0.28 ± 0.10 ; $W = 65$,

$p = 0.025$, $n = 14$), and supporting the body in the tripodal stance (mean HI = 0.31 ± 0.08 ; $W = 83$, $p = 0.010$, $n = 14$).

No correlation between the direction of the preference and the age of individuals was found in male opossums for any of the behaviours (feeding on non-living food: Spearman correlation, $r = -0.12$, $p = 0.712$; feeding on insects: $r = 0.09$, $p = 0.778$; supporting the body in the tripodal stance: $r = -0.17$, $p = 0.594$; manipulating nest material: $r = -0.48$, $p = 0.116$). Female opossums also did not show any statistically significant correlation between the direction of the preference and age for any of the behaviours (feeding on non-living food: Spearman correlation, $r = -0.37$, $p = 0.190$; feeding on insects: $r = 0.05$, $p = 0.852$; supporting the body in the tripodal stance: $r = 0.07$, $p = 0.814$; manipulating nest material: $r = -0.31$, $p = 0.281$).

In contrast to the direction of manual preferences, the strength did not differ between the sexes of the opossums for any of the behaviours (feeding on non-living food: Mann-Whitney U test, $U = 73.5$, $p = 0.605$; feeding on insects: $U = 47.5$, $p = 0.266$; supporting the body in the tripodal stance: $U = 76.0$, $p = 0.699$; manipulating nest material: $U = 80.0$, $p = 0.857$).

No statistically significant correlation between the age and the strength of preferences was found for any of the behaviours (feeding on non-living food: Spearman correlation, $r = -0.07$, $p = 0.722$; feeding on insects: $r = 0.18$, $p = 0.377$; supporting the body in the tripodal stance: $r = -0.04$, $p = 0.859$; manipulating nest material: $r = 0.04$, $p = 0.859$).

5.1.2. Sugar glider, *Petaurus breviceps*

Similarly to grey short-tailed opossums, statistically significant sex differences in the direction of motor preferences in sugar gliders were found in all the behaviours: feeding on non-living food (Mann-Whitney U test, $U = 33.0$, $p = 0.045$), feeding on insects ($U = 20.0$, $p = 0.001$), supporting the body in the tripodal stance ($U = 31.0$, $p = 0.034$) and manipulating nest material ($U = 18.5$, $p = 0.034$). Therefore, the data on males and females were analysed separately in subsequent analyses.

In male sugar gliders, no direction of manual preferences was found for any of the behaviours (feeding on non-living food: mean HI \pm SEM = -0.07 ± 0.14 ; one-sample Wilcoxon signed-rank test, $W = -12$, $p = 0.666$, $n = 12$; feeding on insects: mean HI = -0.09 ± 0.13 ; $W = -17$, $p = 0.530$, $n = 12$; supporting the body in the tripodal stance: mean HI = -0.11 ± 0.15 ; $W = -18$, $p = 0.505$, $n = 12$; manipulating nest material: mean HI = -0.16 ± 0.14 ; $W = -21$, $p = 0.250$, $n = 9$).

Females sugar gliders showed the left-forelimb preference in all the behaviours: feeding on non-living food (mean HI \pm SEM = 0.38 ± 0.15 ; one-sample Wilcoxon signed-rank test, $W = 53$, $p = 0.008$, $n = 11$), feeding on insects (mean HI = 0.32 ± 0.12 ; $W = 49$, $p = 0.014$, $n = 11$), supporting the body in the tripodal stance (mean HI = 0.40 ± 0.16 ; $W = 49$, $p = 0.010$, $n = 11$), and manipulating nest material (mean HI = 0.45 ± 0.18 ; $W = 36$, $p = 0.038$, $n = 10$).

In male sugar gliders, no correlation between the direction of the preference and the age of an individual was found for any of the behaviours (feeding on non-living food: Spearman correlation, $r = -0.06$, $p = 0.845$; catching live insects: $r = 0.33$, $p = 0.297$; supporting the body in the tripodal stance: $r = 0.06$, $p = 0.861$; manipulating nest material: $r = -0.08$, $p = 0.830$). In female sugar gliders no statistically significant correlation between the direction of the preference and the age of an individual was found too for any of the behaviours (feeding on non-living food: Spearman correlation, $r = -0.38$, $p = 0.243$; catching live insects: $r = 0.13$, $p = 0.706$; supporting the body in the tripodal stance: $r = -0.06$, $p = 0.854$; manipulating nest material: $r = 0.11$, $p = 0.742$).

In sugar gliders, sex had no effect on the strength of the preference for feeding on non-living food (Mann-Whitney U test, $U = 47.5$, $p = 0.266$), catching live insects ($U = 47.0$, $p = 0.253$) or supporting the body in the tripodal stance ($U = 49.0$, $p = 0.309$). Manual preferences for manipulating nest material were stronger in females than in males ($U = 19.5$, $p = 0.041$).

No statistically significant correlation between the age of a sugar glider and the strength of its manual preference was found for any of the behaviours (feeding on non-living food: Spearman correlation, $r = -0.06$, $p = 0.782$; catching live insects: $r = 0.07$, $p = 0.737$; supporting the body in the tripodal stance: $r = -0.07$, $p = 0.752$; manipulating nest material: $r = 0.36$, $p = 0.135$).

5.1.3. Goodfellow's tree kangaroo, *Dendrolagus goodfellowi*

In Goodfellow's tree kangaroos, we failed to reveal statistically significant sex differences in the direction of manual preference for any of the behaviours (feeding from the bipedal position: Mann-Whitney U test, $U = 17.5$, $p = 0.541$; feeding from the quadrupedal position: $U = 15.0$, $p = 0.343$; supporting the body in the tripodal stance: $U = 17.5$, $p = 0.541$; autogrooming: $U = 13.0$, $p = 0.223$).

No statistically significant correlation between the age of an individual and the direction of its manual preferences was found for any of the behaviours (feeding from the bipedal position: Spearman correlation, $r = 0.13$, $p = 0.655$; feeding from the quadrupedal position: $r = 0.09$, $p = 0.762$; supporting the body in the tripodal stance: $r = 0.18$, $p = 0.544$; autogrooming: $r = 0.15$, $p = 0.616$).

In the Goodfellow's tree kangaroo, sex did not influence the strength of manual preferences for any of the behaviours (feeding from the bipedal position: Mann-Whitney U test, $U = 22.0$, $p = 0.976$; feeding from the quadrupedal position: $U = 18.0$, $p = 0.603$; supporting the body in the tripodal stance: $U = 17.5$, $p = 0.536$; autogrooming: $U = 17.0$, $p = 0.492$).

No correlation between the age of an individual and the strength of its manual preferences was found for any of the behaviours (feeding from the bipedal position: Spearman correlation, $r = -0.06$, $p = 0.828$; feeding from the quadrupedal position: $r = -0.08$, $p = 0.797$; supporting the body in the tripodal stance: $r = -0.25$, $p = 0.370$; autogrooming: $r = -0.01$, $p = 0.961$).

5.2. The effect of sex and age on manual laterality in bipedal marsupials

5.2.1. Red-necked wallaby, *Macropus (Notamacropus) rufogriseus*

In captive red-necked wallabies, no statistically significant differences in the direction of manual preferences between the sexes were found for feeding from the bipedal position (Mann-Whitney U test, $U = 82.0$, $p = 0.678$), feeding from the quadrupedal position ($U = 86.5$, $p = 0.845$) and supporting the body in the tripodal stance ($U = 74.0$, $p = 0.423$). For autogrooming, the effect of sex on the direction of the preference could not be analysed because of the small number of studied individuals. In captive red-necked wallabies, sex also had no effect on the strength of manual preferences for feeding from the bipedal position (Mann-Whitney U test, $U = 79.0$, $p = 0.574$), feeding from the quadrupedal position ($U = 89.0$, $p = 0.940$) and supporting the body in the tripodal stance ($U = 55.0$, $p = 0.085$).

The effect of the sex on the strength of the preference for autogrooming could not be analysed because of the small number of studied individuals.

In wild red-necked wallabies no statistically significant sex differences in the direction of laterality were found for any of the behaviours (feeding from the bipedal position: Mann-Whitney U test, $U = 40.5$, $p = 0.586$; feeding from the quadrupedal position: $U = 29.0$, $p = 0.578$; supporting the body in the tripodal stance: $U = 33.0$, $p = 0.633$; autogrooming: $U = 13.0$, $p = 0.237$). The sex of the individual did not influence the strength of manual preferences for any of the behaviours, either (feeding from the bipedal position: Mann-Whitney U test, $U = 32.5$, $p = 0.245$; feeding from the quadrupedal position: $U = 18.0$, $p = 0.103$; supporting the body in the tripodal stance: $U = 28.0$, $p = 0.373$; autogrooming: $U = 13.0$, $p = 0.237$).

5.2.2. Eastern grey kangaroo, *Macropus (Macropus) giganteus*

In captive eastern grey kangaroos, no statistically significant sex differences in the direction of manual preferences were found for any of the behaviours (feeding from the bipedal position: Mann-Whitney U test, $U = 129.0$, $p = 0.985$; feeding from the quadrupedal position: $U = 110.0$, $p = 0.357$; supporting the body in the tripodal stance: $U = 95.5$, $p = 1.000$; autogrooming: $U = 24.5$, $p = 0.814$). The sex had no effect on the strength of motor preferences, either (feeding from the bipedal position: Mann-Whitney U test, $U = 127.0$, $p = 0.927$; feeding from the quadrupedal position: $U = 122.0$, $p = 0.620$; supporting the body in the tripodal stance: $U = 95.5$, $p = 1.000$; autogrooming: $U = 24.5$, $p = 0.814$).

In wild eastern grey kangaroos, no statistically significant sex differences in the direction of manual preferences were found (feeding from the bipedal position: Mann-Whitney U test, $U = 32.0$, $p = 0.564$; feeding from the quadrupedal position: $U = 31.0$, $p = 0.137$; supporting the body in the tripodal stance: $U = 48.5$, $p = 0.268$; autogrooming: $U = 79.0$, $p = 0.618$). The strength of manual preferences did not differ significantly between the sexes for any of the behaviours, either (feeding from the bipedal position: Mann-Whitney U test, $U = 34.5$, $p = 0.717$; feeding from the quadrupedal position: $U = 285$, $p = 0.095$; supporting the body in the tripodal stance: $U = 42.5$, $p = 0.144$; autogrooming: $U = 87.0$, $p = 0.899$).

5.2.3. Brush-tailed bettong, *Bettongia penicillata*

No statistically significant sex differences in the direction of motor preferences were found in brush-tailed bettongs for any of the behaviours (feeding on non-living food: Mann-Whitney U test, $U = 24.0$, $p = 0.767$; catching live insects: $U = 18.5$, $p = 0.774$; supporting the body in the tripodal stance: $U = 18.5$, $p = 0.883$; manipulating nest material: $U = 19.5$, $p = 0.605$). The strength of manual preferences for any of the behaviours did not differ between the sexes, either (feeding on non-living food: Mann-Whitney U test, $U = 20.5$, $p = 0.476$; catching live insects: $U = 18.0$, $p = 0.718$; supporting the body in the tripodal stance: $U = 22.5$, $p = 0.897$; manipulating nest material: $U = 18.0$, $p = 0.825$).

5.2.4. Red kangaroo, *Macropus (Osphranter) rufus*

No sex differences in the direction of manual preferences were found in the red kangaroo for any of the behaviours (feeding from the bipedal position: Mann-Whitney U test, $U = 33.0$, $p = 0.369$; feeding from the quadrupedal position: $U = 87.0$, $p = 0.772$; supporting the body

in the tripod stance: $U = 19.0$, $p = 0.199$; autogrooming: $U = 32.0$, $p = 0.301$). No effect of the sex on the strength of manual preferences was found, either (feeding from the bipedal position: Mann-Whitney U test, $U = 38.0$, $p = 0.608$; feeding from the quadrupedal position: $U = 83.0$, $p = 0.634$; supporting the body in the tripod stance: $U = 15.5$, $p = 0.096$; autogrooming: $U = 37.0$, $p = 0.522$).

5.3. Conclusion

The effect of the sex of an individual on the expression of its manual preferences was revealed in two studied species. In the grey short-tailed opossum and the sugar glider sex differences in the direction of manual preferences were found in all the behaviours. Females of both species were more inclined to use the left forelimb than males. In the other five species of marsupials studied the sex did not influence manual laterality.

The effect of sex on manual preferences of placentals also varies between species [Pfannkuche et al., 2009]. In some primates no sex differences in the manifestations of motor laterality were found [McGrew, Marchant, 1997; Vauclair et al., 2005; Meunier, Vauclair, 2007; Lhota et al., 2009]. At the same time, right-handedness is more characteristic of females than of males in many primates [Ward, 1995; Corp, Byrne, 2004; Bennett et al., 2008; Sommer et al., 2008; Llorente et al., 2011; Meguerditchian et al., 2012] and some other mammals: dogs [Wells, 2003], cats [Wells, Millsopp, 2009], and horses [McGreevy, Thomson, 2006]. The results of our study show that the effect of sex on the direction of manual preferences is different in the studied species of marsupials and in placentals. Differences in the manual preferences in females and males of placentals are presumably associated with the sex dimorphism in the size of corpus callosum [De Lacoste, Woodward, 1988; Phillips et al., 2007]. For instance, sex and handedness were shown to influence the size of corpus callosum in capuchin monkeys [Phillips et al., 2007]. Marsupials have no corpus callosum, and their brain hemispheres are connected via alternative interhemispheric pathways [Heath, Jones, 1971]. Possibly, it is the morphological differences in the structures underlying the sex-related specificity of lateralised behaviour that result in a different effect of sex on the direction of manual preferences in placentals and in marsupials. Further research is necessary to elucidate this issue.

The effect of age on the manifestations of manual laterality was studied in three species of marsupials for which information about the exact age of individuals was available. In the grey short-tailed opossum, the sugar glider and the Goodfellow's tree kangaroo no dependence between the age of individuals and the expression of manual preferences was found. In the red-necked wallaby and the eastern grey kangaroo, the use of one forelimb was studied in different behaviours in the young and in the adults. The young of both species were studied at two developmental stages: young-at-foot and pouch young. Since newly born marsupials have to climb or crawl all the way to the mother's teat, forelimbs and the nervous structures controlling them develop much earlier in their ontogenesis than in most placentals [Cooper, Stepan, 2010]. In marsupials and especially in macropods (Macropodidae), even pouch young display a complex dexterity [Dawson, 2012]. This means that manual laterality in marsupials can be investigated at the earliest stages of postnatal development.

In this work we studied manual preferences for manipulating plant food in the pouch young of macropods (Fig. 4b). Pouch young of the red-necked wallaby and the eastern grey kangaroo showed both individual and group-level manual laterality. Both species demon-

strated a group-level left-forelimb preference for manipulating food objects. This means that in these species the left-forelimb preference for feeding is characteristic of both adults and young. In adult red-necked wallabies, the left-forelimb preference was observed for feeding from the bipedal position but not for feeding from the quadrupedal position. The posture of a young wallaby that has freed its head and forelimbs from the mother's pouch is quite similar to the bipedal posture of an adult: forelimbs are free (not touching the ground) and the body is vertically oriented. This indicates that the young and the adults of the red-necked wallaby have the same direction of manual preferences in actions with similar characteristics.

In young-at-foot of the red-necked wallaby and the eastern grey kangaroo lateralised limb use for pulling down the mother's pouch during suckling was studied (Fig. 4c) [Giljov et al., 2012c]. In most cases after pulling down the edge of the mother's pouch with both forelimbs in the beginning of suckling, the young lowered the right forelimb, continuing to pull down the edge of the pouch by the left one. The young of the red-necked wallaby immediately lowered the free paw on the ground, using it as a prop. This division of functions between the forelimbs in the young agrees with the adults' preference to manipulate mostly with the left forelimb, using the right forelimb for support. However, in the eastern grey kangaroo, with its more pronounced disproportion of forelimbs and hind limbs than in wallabies [Hume et al., 1989], the forelimb uninvolved into pulling down the mother's pouch during suckling did not touch the ground and so did not serve as a prop. In this case, only the manipulative function of the forelimb remaining in the pouch was lateralised. Possibly, in the red-necked wallaby, too, the laterality of manipulative functions of the forelimb plays the most important role in this behaviour. In other words, the choice of the forelimb for pulling down the mother's pouch has an overriding influence, while the other forelimb plays a complementary, accessory role. Manual preferences in the young and the adults seem to arise from the same phenomenon. The left-forelimb preference for manipulation is present in the red-necked wallaby and the eastern grey kangaroo both at the stage of pouch young and at the following stages of development [Giljov et al., 2017].

MANUAL LATERALITY IN CAPTIVE AND WILD MARSUPIALS

Two species of marsupials, the red-necked wallaby and the eastern grey kangaroo, were observed both in zoos and in nature [Giljov, 2014; Giljov et al., 2012c, 2015a]. In these two species we compared the manual preferences in captive and in wild individuals. Both the strength and the direction of manual preferences for each behaviour were compared using Mann-Whitney U test [Mann, Whitney, 1947].

6.1. Comparison of laterality in captive and wild red-necked wallabies, *Macropus (Notamacropus) rufogriseus*

Comparison of the direction of manual laterality in captive and wild individuals revealed no statistically significant differences for any of the behaviours (feeding from the bipedal position: Mann-Whitney U test, $U = 232.0$, $p = 0.419$; feeding from the quadrupedal position: $U = 150.5$, $p = 0.057$; supporting the body in the tripodal stance: $U = 200.0$, $p = 0.325$; autogrooming: $U = 55.5$, $p = 0.652$; Fig. 29).

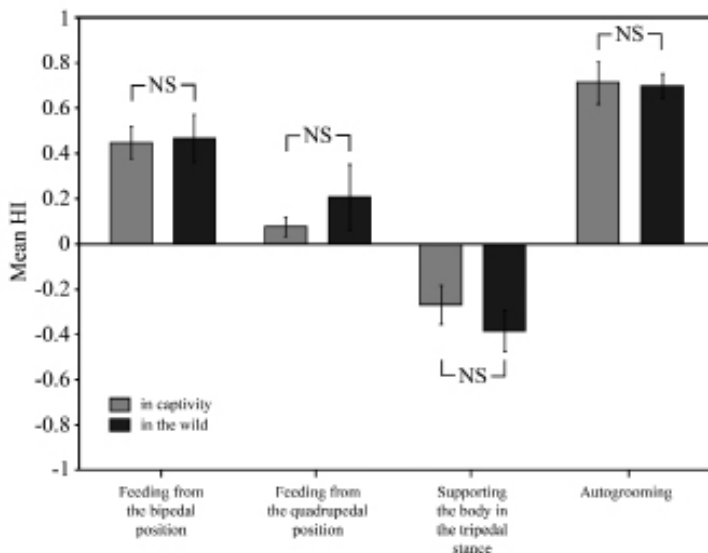


Fig. 29. Comparison of the direction of manual laterality in captive and wild individuals of the red-necked wallaby. HI — handedness index: positive values — left-forelimb bias, negative values — right-forelimb bias; NS — not significant.

The strength of manual laterality for feeding from the quadrupedal position was higher in wild individuals than in captive ones ($U = 18.0, p < 0.001$). No differences were found for three other behaviours (feeding from the bipedal position: $U = 212.5, p = 0.219$; supporting the body in the tripodal stance: $U = 200.0, p = 0.325$; autogrooming: $U = 55.5, p = 0.652$; Fig. 30).

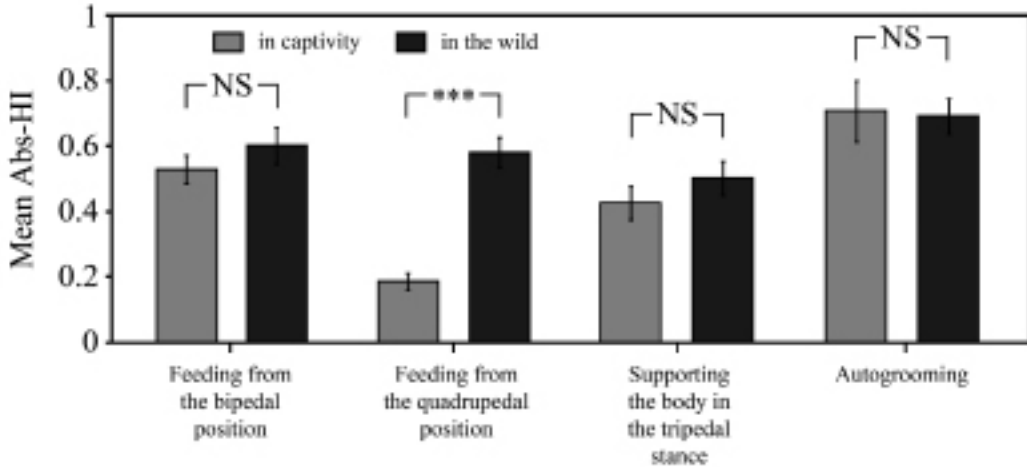


Fig. 30. Comparison of the strength of manual laterality in captive and wild individuals of the red-necked wallaby. Abs-HI — absolute values of handedness index;; *** $p < 0.001$; NS — not significant.

6.2. Comparison of laterality in captive and wild eastern grey kangaroos, *Macropus (Macropus) giganteus*

No significant differences in the direction of manual laterality in captive and wild individuals were found for any of the behaviours (feeding from the bipedal position: Mann-Whitney U test, $U = 312.0, p = 0.981$; feeding from the quadrupedal position: $U = 350.5, p = 0.699$; supporting the body in the tripodal stance: $U = 305.0, p = 0.428$; autogrooming: $U = 177.0, p = 0.323$; Fig. 31).

The strength of manual preferences did not differ in wild and captive individuals, either (feeding from the bipedal position: Mann-Whitney U test, $U = 300.5, p = 0.810$; feeding from the quadrupedal position: $U = 264.5, p = 0.067$; supporting the body in the tripodal stance: $U = 264.5, p = 0.130$; autogrooming: $U = 165.0, p = 0.198$; Fig. 32).

6.3. Conclusion

Conditions of the environment are known to influence manual preferences [Hopkins, 2006; Lhota et al., 2009; Rogers, 2010; Schnoell et al., 2014]. In this work, both captive and wild animals were investigated. In the red-necked wallaby and the eastern grey kangaroo the direction of manual laterality was the same in captive and wild individuals. A similar direction of

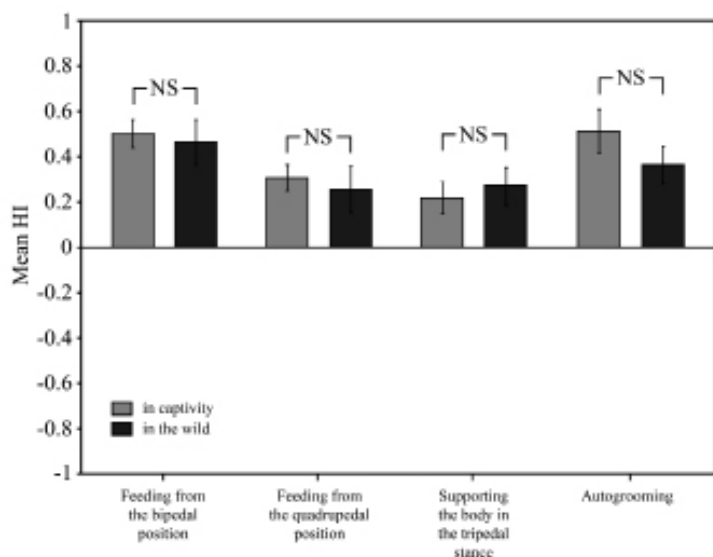


Fig. 31. Comparison of the direction of manual laterality in captive and wild eastern grey kangaroos. Designations as in Fig. 29.

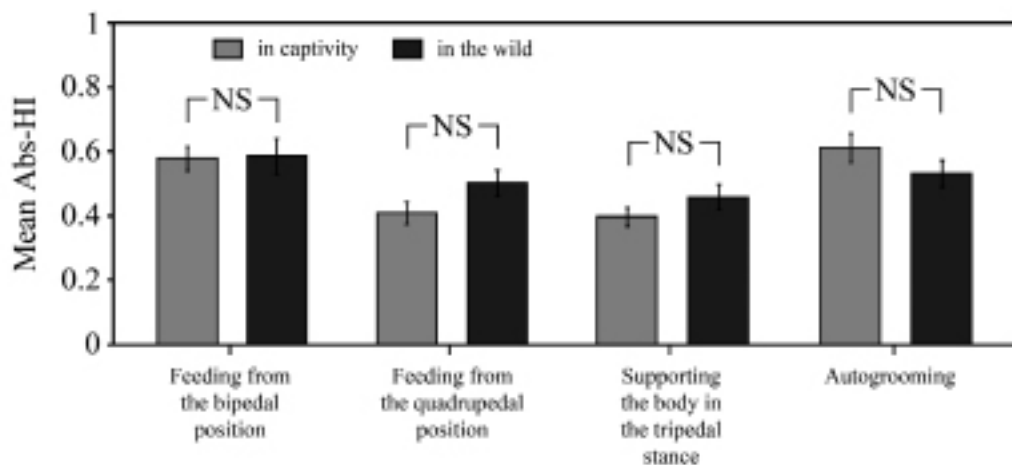


Fig. 32. Comparison of the strength of manual laterality in captive and wild eastern grey kangaroos. Designations as in Fig. 30.

preferences in all studied behaviours (Fig. 17, 21) indicates that manual preferences are stable in these species. Differences in the strength of manual preferences in captive and wild animals were found only in the red-necked wallaby and only for one type of behaviour (feeding from the quadrupedal position). In most studied primate species, laterality differs depending on the conditions: manual preference in wild individuals may be weaker [Marchant, McGrew, 1996; Mittra et al., 1997] or stronger [Hopkins et al., 2007] than in captive conspecifics. This suggests that captivity has a lesser effect on the manual preferences of marsupials as compared with primates. In general, manual preferences of marsupials can be said to be more stable than those of the placentals studied in this respect.

INTERSPECIFIC DIFFERENCES IN MANUAL LATERALITY IN MARSUPIALS

7.1. Comparative characteristics of manual laterality in the studied species of marsupials

By analogy with the classification of ‘levels of laterality’ [McGrew, Marchant, 1999] used for estimation of the degree of handedness in primates [Lhota et al., 2009; Leca et al., 2010], the five-level system was applied to classify the degree of manual laterality in marsupials [Giljov et al., 2015a]. This classification system takes into account both the ratio of lateralised and non-lateralised individuals and the direction of laterality. The use of such a classification for the interspecies comparison seems to be reasonable, because it summarizes the manifestation of manual laterality in a species. To put it simply, level 1 corresponds to the weakest expression of manual laterality, while level 5 defines manual laterality in its most pronounced form. Level 1 is defined as when the majority of individuals are non-lateralised, i.e. do not display forelimb preferences in any type of behaviour; while level 2 is defined as when there is no significant difference between the number of lateralised and non-lateralised individuals. When the majority of individuals are lateralised, but the number of left- and right-handed individuals does not differ significantly, the species was classified as having laterality level 3. Level 4 is defined as follows: there are more lateralised than non-lateralised individuals and more left- or right-handers among lateralised individuals in the majority of behaviours; the direction of group-level laterality varies depending on the type of behaviour. Finally, the highest level (5) is defined as when the majority of individuals are left- or right-handed and the direction of laterality is similar in all or the majority of behaviours. For interspecific comparison, we determined the laterality level in each of studied marsupial species based on the data on four behaviours, in which individual and group-level laterality was statistically assessed. The full range of manual behaviours was not investigated in all species studied. However, the most common and likely representative types of unimanual behavior for each marsupial species were included in the interspecies comparison [Giljov et al., 2015a].

In the grey short-tailed opossum, the sugar glider and the Goodfellow’s tree kangaroo the number of individuals displaying individual manual preferences did not differ significantly from that of individuals without manual preferences in all the studied behaviours. According to the classification of “laterality levels” [Giljov et al., 2015a], this corresponds to level 2. In the red-necked wallaby the number of lateralised individuals for majority of behaviours significantly exceeded that of non-lateralised ones, while the number of individuals preferring one forelimb was greater than that of individuals preferring the other forelimb. The

direction of the bias (more left-handers vs. more right-handers) depended on the behaviour. These manual preferences correspond to laterality level 4. In the eastern grey kangaroo, the red kangaroo and the brush-tailed bettong, there were considerably more lateralised individuals than non-lateralised ones for most of the behaviours. In these three species the number of left-handers was greater than that of right-handers in all the behaviours. These consistent manual preferences correspond to level 5. This means that the marsupial species in our study were characterised by different levels of laterality according to the classification [Giljov et al., 2015a] (Fig. 33).

In placental mammals, interspecific differences in manual laterality cannot be explained by phylogenetic relationships [Scheumann et al., 2011; Meguerditchian et al., 2012]. Congeneric species may show strikingly different patterns of motor preferences, while species from different families may demonstrate similar laterality patterns [Ströckens et al., 2013]. Our observations indicate that this conclusion is also true for marsupials. Representatives of different families — the grey short-tailed opossum (Didelphidae), the sugar glider (Petauridae) and the Goodfellow's tree kangaroo (Macropodidae) — are characterised by the same level of laterality, while representatives of the same family — the Goodfellow's tree kangaroo, the red-necked wallaby, the eastern grey kangaroo and the red kangaroo (Macropodidae)—are characterised by different laterality levels.

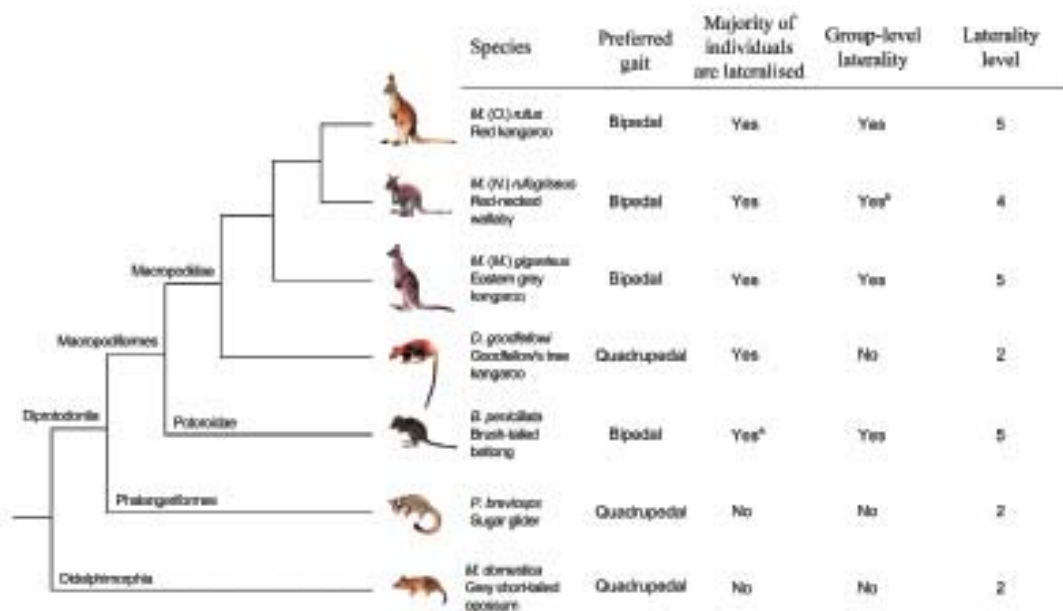


Fig. 33. Manual laterality in marsupials. Taxonomic position of the studied species is shown on a simplified cladogram of extant marsupials (Marsupialia). The following information is given for each species: prevailing gait, presence/absence of individual and group-level laterality ($p < 0.05$), laterality level according to a five-level classification. Figure from Giljov et al., 2015a.

7.2. The effect of gait and body posture on manual laterality

Preferred gait is proposed to be one of the key factors determining the manifestations of manual laterality in placentals [Ward, 1995]. The bipedalism theory postulates that the emergence of a marked handedness in primates was associated with the adoption of bipedal locomotion [Ward, 1995; Westergaard et al., 1998; Corbetta, 2003]. More bipedal species (as regards posture and locomotion) are characterised by a stronger manual laterality for feeding [Dodson et al., 1992; Ward et al., 1993].

Marsupial species under study had various gaits. Grey short-tailed opossums and sugar gliders move only quadrupedally [Pridmore, 1992; Shapiro, Young, 2010]. However, sugar gliders, in contrast to grey short-tailed opossums, often assume bipedal stance when not moving. Goodfellow's tree kangaroos, though capable of bipedal locomotion, mainly move quadrupedally. They have lost many characters of bipedal macropods in the course of evolution because of transition to life on trees [Flannery et al., 1996; Martin, 2005; Kear et al., 2008]. The other species use mainly bipedal locomotion. Red-necked wallabies move bipedally at high and middle speeds but usually assume a quadrupedal position when moving slowly or during grazing [Hume et al., 1989]. The eastern grey kangaroo, the red kangaroo and the brush-tailed bettong are the most bipedal of the studied species. Disproportion of the hind limb bones and other adaptations to bipedalism in the eastern grey kangaroo and the red kangaroo are the strongest out of all modern Macropodidae [Kear et al., 2008; Dawson, 2012]. The brush-tailed bettong is also one of the most bipedal species of its family; it uses quadrupedal locomotion very rarely [Webster, Dawson, 2003]. Our observations showed that bettongs almost never manipulated objects (food or nest material) from the quadrupedal position. In general, the level of laterality correlates with the preferred gait of the species: the highest level 5 is characteristic of bipedal marsupials, and the lowest level 2, of quadrupedal marsupials (Fig. 34). Group-level laterality is found only in species with a predominantly bipedal gait (Fig. 33; Giljov et al. [2015a]). Similarly to primates [Dodson et al. 1992; Ward et al., 1993; Ward, 1995], the strongest expression of manual laterality in the studied marsupials was found in the most bipedal species.

The effect of the body posture during the performance of actions on manual laterality differed between the species of macropods in our study. While in the red-necked wallaby the number of left-handers did not differ from that of right-handers during feeding from the quadrupedal position and no group-level laterality was observed, in the eastern grey and the red kangaroo most individuals showed the left-forelimb preference regardless the position from which they manipulated food. It seems that in the most bipedal species the expression of manual laterality does not decrease even when they perform actions from the quadrupedal position. A similar tendency can be seen in primates, too. Body posture influences manual preferences in species, which use bipedal locomotion comparatively rarely [Hopkins, 1993; Ward et al., 1993; Westergaard et al., 1997; Blois-Heulin et al., 2007; Braccini et al., 2010]. However, humans, a species characterised by a balanced obligate bipedalism [Skoyles, 2006; Niemitz, 2010], show a marked right hand preference for manipulating food both from the bipedal and from the quadrupedal position [Westergaard et al., 1998]. At the same time, in quadrupedal mammals such as cats [Konerding et al., 2012], grey mouse lemurs [Scheumann et al., 2011], and tree shrews [Joly et al., 2012] weak manual preferences were observed both for feeding in the (typical) quadrupedal body posture and for manipulating food after an artificially induced adoption of the bipedal posture. Similarly, the bipedal posture did not result

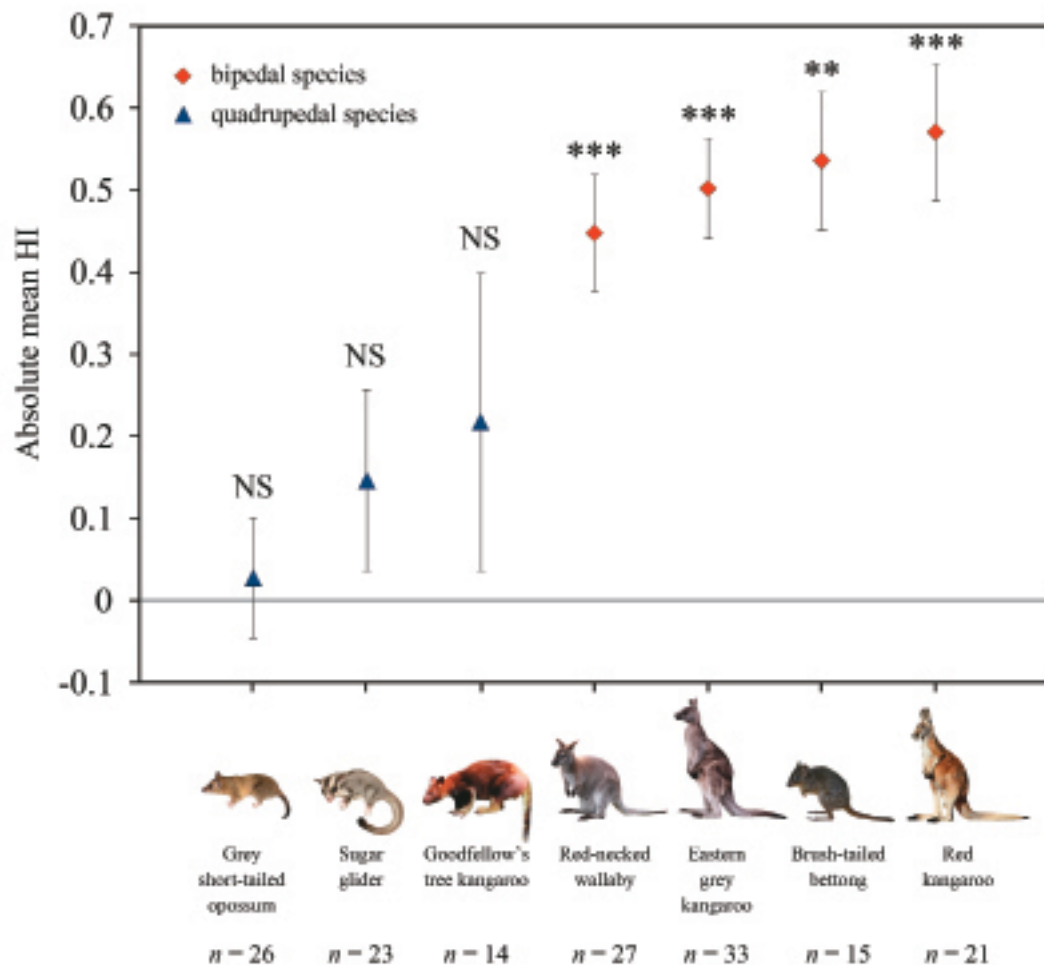


Fig. 34. Group-level laterality in the studied species of marsupials. Absolute values of mean handedness indices (HI) in bipedal and quadrupedal species during feeding. Species displaying group-level laterality are marked with asterisks: ** $p < 0.01$; *** $p < 0.001$.

in stronger manual preferences in Goodfellow's tree kangaroos, which mostly use quadrupedal locomotion [Martin, 2005; Kear et al., 2008]. Thus, in the studied bipedal marsupials a marked manual laterality was observed even in the quadrupedal body posture, while in a quadrupedal species it was weak even in the bipedal posture. The similarities in the manifestations of manual laterality between marsupials and placentals indicate the universal nature of the postural effect on the manual laterality in mammals.

Conclusion

We studied manual laterality in seven species of marsupials and compared our results with the available data on manual laterality in placentals. Both differences and similarities in manual preferences in these two mammal groups were found. The effect of the sex on the direction of laterality in the studied marsupials differed from that in most placentals. Further research is necessary to understand the causes of sex differences in the manifestations of manual laterality in marsupials. Several tendencies in the lateralised use of forelimbs were similar in marsupials and placentals: the divisions of functions between the limbs, the effect of the body posture on the manifestation of manual preferences, the differences in manual preferences between species with different locomotor characteristics. These similarities indicate the existence of common factors underlying individual and group-level laterality in mammals. The results obtained on the marsupial young support the hypothesis that lateralised limb use is expressed at the early stages of the postnatal development. In general, the results of this study broaden our understanding of the occurrence of manual laterality in mammals. Combined with the results of earlier studies on placentals, the data on the interspecific differences in the motor preferences of marsupials support the idea about the plasticity of manual laterality under the impact of ecological factors [Bisazza et al., 2000; Malashichev, 2006b; Scheumann et al., 2011].

Further research on this topic may include in-depth studies of manual preferences in marsupials with the aim of testing the hypotheses suggested in this work. An insight into the evolution of lateralised behaviour might be gained from the study of motor preferences in the long-nosed potoroo, *Potorous tridactylus*, a species from the family Potoroidae with a predominantly quadrupedal gait [Windsor, Dagg, 1971]. Its comparison with the brush-tailed bettong, a bipedal species from the same family studied in this work, would be a test of the hypothesis about the correlation between the bipedal locomotion and strong manual preferences. Complex bimanual activity can be studied on representatives of the family Phalangeridae, marsupials with the most developed manipulative capacities [Iwaniuk et al., 2000], with the use of experimental techniques developed in primate research [Hopkins, 1995; Meguerditchian et al., 2013]. This would allow a direct comparison of manual laterality in marsupials and placentals in the same types of actions. The study of other groups of mammals using bipedal locomotion, possibly elucidating a link between the gait and the manual preferences, is another promising direction of research.

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Abbreviations and Symbols

Abs-HI	Absolute handedness index
HI	Handedness index
l	Number of acts of the left forelimb use
r	Number of acts of the right forelimb use
A	Ambipreferent (No preference)
L	Left-forelimb preference
R	Right-forelimb preference
<i>n</i>	Number of studied individuals
♀	Female
♂	Male

Terms and Definitions

The following terms and definitions are used in this monograph.

1. ***Absolute handedness index (Abs-HI)***: Absolute values of handedness index (handedness index irrespective of the plus/minus sign) reflect the strength of the manual preference without considering the direction of the preference.
2. ***behavioural lateralisation***: Various left-/right biases in behavioural responses of animals such as, for example, the preference to use one of the paired limbs for certain tasks or a more marked reaction to a stimulus presented in the field of vision of one of the eyes.
3. ***bimanual actions***: Actions with simultaneous involvement of two forelimbs. In studies of manual preferences, this term is usually applied to actions in which the left and the right forelimb perform different functions, e.g., one hand is holding the container with food and the other hand reaches for food and brings it to the mouth.
4. ***bipedal locomotion***: Locomotion with the use of two hind limbs only.
5. ***bipedal posture***: Posture of an animal standing on two hind limbs only.
6. ***bipedality (degree of bipedality) of a species***: The degree in which bipedal locomotion and bipedal posture are characteristic of a species as compared to other species.
7. ***contralateral***: Situated at the opposite side of the body. For example, the left hemisphere is contralateral to the right hand.
8. ***direction of laterality***: This term is used to define the bias (left-sided or right-sided) of laterality. In case of manual laterality, the direction of laterality (the direction of manual preferences) is reflected in the values of the handedness index.
9. ***handedness index (HI)***: An index used to assess manual preferences of animals. In the present study an individual handedness index (HI) was calculated for each subject in each type of behaviour with the following formula: $(\text{left-forelimb use} - \text{right-forelimb use}) / (\text{left-forelimb use} + \text{right-forelimb use})$. HI scores range from -1.0 to $+1.0$, with negative values indicating the right-forelimb bias and positive values the left-forelimb bias.
10. ***lateralised (non-lateralised) individual***: In the present study this term was defined as an individual that displays (does not display) the left or the right limb preference.
11. ***lateralised limb use***: Unequal use of the left and the right limb.
12. ***manual laterality at the individual level (individual laterality)***: Preference of the left or the right forelimb displayed by an individual.
13. ***manual laterality at the group level (group-level laterality)***: Lateral bias in the lateralised forelimb use in the sample. To assess group-level laterality, the number of left-handers in the group is compared to that of right-handers or/and the mean values of laterality measures, e.g., handedness index, are tested for the presence of a left-/right bias.
14. ***manual laterality***: Asymmetrical participation of paired forelimbs in motor tasks.
15. ***motor asymmetry (motor laterality)***: Asymmetry in the motor activity of an organism.

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- 16. quadrupedal locomotion:* Locomotion with the use of two hind limbs and two forelimbs.
- 17. quadrupedal posture:* Posture of an animal standing on two forelimbs and two hind limbs.
- 18. strength of laterality:* This term is used to define the degree of the expression of laterality regardless of its direction. In case of manual laterality, the strength of laterality (the strength of manual preference) is reflected in the absolute values of the handedness index.
- 19. subgroup-level laterality:* Laterality displayed only by some of the studied individuals, which are united by a common character, e.g., belong to the same sex.
- 20. tripedal stance:* Posture of an animal standing on two hind limbs and a forelimb.
- unimanual actions* (unimanual behaviours): Actions (behaviours) involving the use of one forelimb.

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