THE EVOLUTION OF SKILLED FORELIMB MOVEMENTS IN CARNIVORANS.

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ABSTRACT

Emancipating the forelimbs from locomotion for use in other activities, such as food manipulation, is a major evolutionary milestone. A variety of selective forces and evolutionary correlates may influence the evolution of various degrees of skill with which the forelimbs are used. Using the order Carnivora as a test group, I assessed the relative influence of six factors: relative brain size, neocortical volume, manus proportions, body size, phylogenetic relatedness, type of locomotion and diet. I developed a rating system to describe the dexterity of individual species and compared the scores to the six factors using modern comparative methods. Only phylogeny and diet were significantly correlated with forelimb dexterity. More specifically, forelimb dexterity tends to be higher in caniform than in feliform carnivorans and decreases with increasing specialisation on vertebrate prey. I conclude that food handling and feeding niche breadth have a significant effect upon the evolution of skilled forelimb movements.

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(Sir Perceval, Monty Python and the Holy Grail)

"Even in the psychological field, living organisms are phylogenetically derived entities whose specific origin and form can only be interpreted in the light of their phylogenetic history."

(Lorenz, 1941; p.16)

CHAPTER ONE

GENERAL INTRODUCTION

Skilled forelimb movements, which include the ability to reach for objects, hold them in a hand/forepaw and manipulate them with the digits, are proposed to be highly developed in primates relative to other taxa, with the apex reached by humans (Napier, 1960). Although primates are certainly skilled in the use of their forelimbs, similar degrees of skill, or dexterity, have been achieved by members of other mammalian groups. For example, Norway rats (*Rattus norvegicus*) have been shown to execute complex digit movements in the manipulation of a variety of food items (Whishaw and Coles 1996; Whishaw and Gorny 1994). In fact, members of at least 5 mammalian orders other than primates, as well as some non-mammalian species (Gray et al. 1997), are known to perform skilled forelimb movements. This distribution raises the issue of whether these movement patterns have arisen independently within each lineage (i.e. analogy or homoplasy) or whether such behaviour has arisen early in mammalian evolution and become subsequently lost or elaborated upon in different lineages (i.e. homology) (Futuyma 1986).

This evolutionary question is particularly important in behavioural neuroscience because the overlapping patterns of behavioural and neural evolution with regard to forelimb use have been frequently cited as supporting evidence for possible causal relationships between structure and function. For example, based upon the pattern of corticospinal tract anatomy and digital dexterity across 60+ species of mammals, Heffner and Masterton (1975, 1983) concluded that both the length and depth of corticospinal fibres are positively correlated with dexterity of the digits. Similarly, Eccles (1989), Hopson (1977) and Nudo and Masterton (1990) have proposed that relative brain size and dexterity are positively correlated. One of the many problems with these analyses is that they have all assumed that skilled forelimb movements have evolved independently throughout tetrapod evolution, but the structural changes involved are similar. That is, skilled forelimb movements have evolved in parallel in a number of different mammalian and non-mammalian taxa and therefore the neural control of the movements is similar. To treat skilled forelimb movements as a homoplastic trait, rather than a homologous one, requires some empirical proof that changes in the trait follow a pattern of convergence/parallelism, rather than possession of traits held by a common ancestor (Futuyma 1986). Once it has been determined whether skilled forelimb movements are homologous or not in tetrapods, it may then be possible to assess the relative importance of various selective forces (e.g. diet, locomotion) and neural correlates (e.g. spinal descending pathways, relative brain size) with respect to their diversification.

The Comparative Analysis of Motor Patterns

Interest in the interspecific variation of behaviour has long been a major focus of biologists (e.g. Darwin 1872). Early attempts to examine behavioural patterns comparatively tended to concentrate upon displays, or similar behaviours, which were 'stereotypical' in structure (Lorenz 1941). Despite the potential for this approach to increase our understanding of behavioural evolution, it was highly criticised (e.g. Atz 1970). The most common criticism was that it was difficult to prove whether the behaviours were homologous or not. In fact, it has been suggested that behaviours are so labile that it may be impossible to homologise them (Atz 1970; de Queiroz and Wimberger 1993). Thus, interspecific differences in behaviour were subsequently viewed as adaptive, with little to no phylogenetic component.

A significant problem with this post-Lorenzian approach to behaviour is that it ignores the contribution that phylogenetic ancestry can have on the expression of behaviours in extant phenotypes. Until relatively recently, the effects of phylogeny on the expression of behaviours were ignored (Thornhill and Alcock 1983; Yokel 1986) or dismissed as relatively unimportant (Nudo and Masterton 1990). This begs the question posed by McLennan et al. (1987): "Does phylogeny,..., contribute nothing to studies surrounding the often elusive mechanisms involved in the evolution of behavioural characters?" (p. 2181).

More recently there has been a philosophical backlash to the 'post-Lorenzian' approach brought on by the advent of a host of comparative methods. As a result of this renewed interest in comparative studies, cladistic analyses have been performed on a number of behaviour-based data sets to test the concept that behaviours cannot be defined as homologous. Given that the similarity between phylogenetic trees derived from different data sets is the best indicator of phylogenetic utility (Bledsoe and Raikow 1990; Penny et al. 1982; Zink and Avise 1990); comparing behaviourally based trees with independently derived trees would give some indication as to whether behaviours contain significant amounts of phylogenetic information. The results of these analyses clearly indicate that behaviours map reasonably well onto independently derived trees (e.g. Crowe et al. 1992; Prum 1990; Winkler and Sheldon 1993); and that behaviour-derived trees are more congruent with independently-derived trees than would be expected by chance (deQueiroz and Wimberger 1993; Kennedy et al. 1996; McLennan et al. 1987; Paterson et al. 1995; Slikas 1998). Thus, although the behaviours may be difficult to homologise, the fact that the distribution of most behaviours is congruent with independently derived phylogenies, suggests that evolutionary history plays an integral role in behavioural expression. Interspecific comparisons should therefore utilise methods which incorporate phylogenetic information to address the question being asked.

Recently, a host of comparative methods have been developed for this express purpose (Harvey and Pagel 1991). They range from techniques which can estimate the amount of variation attributable to phylogeny (Diniz-Filho et al. 1998; Gittleman and Kot 1990; Gittleman and Luh 1992), to methods which incorporate phylogenetic information (Felsenstein 1985; Grafen 1989) and examine evolutionary patterns (Maddison and Maddison 1992). Although most of these techniques have been used to investigate various ecological hypotheses, these methods are being increasingly used to examine behaviour. Just as with Lorenz's (1941) original work, these studies tend to focus upon displays (e.g. Paterson et al. 1995; Slikas 1998) and gross behavioural categories (e.g. parental care (Gittleman and Decker 1994)). To date there have been few phylogenetic examinations of the evolution of non-display behaviour (for some exceptions see Dobson 1985; Greene 1994; Langtimm and Dewsbury 1991; Pellis and Iwaniuk 1999a, 1999b). Although many would claim that such behaviours are evanescent and change markedly within relatively few generations, there is no empirical support for this hypothesis. In fact, if this were to occur, then the behaviour of captive individuals, and especially laboratory animals, would be qualitatively different from that of wild individuals. To the contrary, motor behaviours (i.e. non-display behaviours) have been shown to be consistent between both captive and wild individuals with only quantitative alterations in the execution of the behaviours (e.g. duration, frequency) (Pasztor et al. submitted). Thus, just as with display behaviours, motor behaviours are subject to selection pressures such that a significant portion of their variation can be attributed to phylogenetic relatedness.

Although there are many behaviours which could be examined to demonstrate how modern comparative methods could be used to elucidate the evolution of non-display behaviours, in my thesis I examined skilled forelimb movements, as outlined above. The skill and complexity with which these movements are performed is referred to as 'dexterity' and the interspecific variability in dexterity (Bishop 1964; Ivanco et al. 1996; Iwaniuk 1996; Landy 1997; Whishaw et al. 1998a) makes skilled limb movements an ideal behaviour for examination with modern comparative methods.

The Evolution of Skilled Forelimb Movements

Prior to the examination of interspecific variation in dexterity, and its evolution, it is necessary to develop a rating system of dexterity such that each species could be assigned a numerical value. The only index currently available (Heffner and Masterton 1975, 1983; Napier 1960, 1961) has been shown to be problematic for one main reason: it was based on external manus morphology rather than behaviour. In this index, species which have a manus shape more similar to humans score relatively higher than species which have a manus dissimilar to humans (Napier 1960, 1961). Thus, there is an implicit assumption, which remains unproven, that the gross structure of the forepaws is directly related to their manipulative capabilities. My own research has, in fact, demonstrated that dexterity scores based on manus morphology do not correspond with actual ability. For example, such scores underestimate the dexterity of kangaroos (Iwaniuk 1996; Iwaniuk et al. 1998) and overestimate the abilities of the raccoon (*Procyon lotor*) (Iwaniuk and Whishaw 1999). Similarly, the laboratory rat (*Rattus norvegicus*) (Whishaw and Coles 1996; Whishaw and Gorny 1994) and chimpanzees (*Pan paniscus*, *P. troglodytes*) (Christel 1993; Christel et al. 1998) have been shown to be incorrectly scored. For this, and other reasons (see Chapter 2), the Heffner and Masterton (1975, 1983) index is inappropriate for use in assigning actual dexterity to different species. To examine the evolution of dexterity, it is necessary, however, to have some sort of numerical coding system. Therefore, in the first portion of my thesis such a system is developed which is used in subsequent chapters to examine the possible selective mechanisms involved in the diversification of dexterity in mammals.

Numerous attempts have been made to explain the mechanisms responsible for the evolution of high degrees of forelimb dexterity in different mammalian taxa. Firstly, it has been suggested that relative brain size is positively correlated with forelimb dexterity (Eccles 1989; Gittleman 1986a; Hopson 1977). The rationale for such a relationship is based upon Jerison's (1973) principle of proper mass which states that the amount of neural tissue responsible for a particular function is equivalent to the amount of processing required for that function to occur. That is, with increasing behavioural complexity, there is a correlated increase in the amount of neural substrate responsible for the execution of the behaviour. The apparent overlap between highly encephalised species (i.e. big-brained) and dexterity has been taken as supporting evidence for this hypothesis, but it has not been specifically tested.

Secondly, it has been suggested that the relative length of the digits is a reliable indicator of forepaw dexterity (Napier 1960, 1980). Specifically, the longer the digits are, the better the grasping ability and, therefore, the higher the dexterity. In a similar fashion to the previous theory, the evidence for this is primarily cursory observations of behaviour overlapped with gross manus morphology.

Thirdly, phylogenetic association has also been suggested to be related to variation in dexterity. Evidence for this theory comes from a number of studies. For example, Bishop (1964) demonstrated that prosimians belonging to the same subfamily had more similar reaching, grasping and manipulatory movements than to members of other subfamilies. Thus, bushbabies (*Galago, Galagoides* and *Otolemur* spp.) are more similar to one another than they are to lemurs (*Eulemur, Lemur* spp.). Similarly, Whishaw et al. (1998) have shown that the forelimb movements of sciurid rodents resemble one another more than they do muroid rodents. Lastly, in a comparative study of callitrichids, Singer and Schwibbe (1999) provide evidence that there are genus-specific (*Callithrix, Leontopithecus, Saguinus*) patterns of forepaw use. Thus, it would appear that a significant amount of the variation in dexterity may be attributable to phylogeny.

Fourthly, it has been proposed that high forelimb dexterity is more likely to occur in arboreal forms than non-arboreal forms (Wood-Jones 1916). This was originally based upon an examination of arboreal marsupials (Wood-Jones 1916), but has been subsequently extrapolated to primates and other mammalian taxa (Cartmill 1985). Although the grasping ability of some didelphid marsupials and primates has been qualitatively assessed recently (Lemelin 1999), there is little other than anecdotal evidence that grasping during locomotion can be translated into higher dexterity.

Lastly, predatory behaviour may promote the evolution of high forelimb dexterity (Gittleman 1986a). More specifically, the behavioural requirements for the successful capture of small vertebrate prey and the need to rapidly manipulate prey into an appropriate position to deliver a killing bite therefore acts as a significant selection pressure promoting high forelimb dexterity. This is despite the fact that speed of movements does not necessarily mean that they are skilled (see Chapter 4).

There are two main problems with these competing theories. Firstly, contrary to the suggestions by the authors, they are not mutually exclusive. Both the structure and behaviour of extant phenotypes are the result of a suite of different selection pressures of varying intensities. Therefore, all five mechanisms could be acting in concert, albeit at varying degrees of influence, to produce the observed variability in forelimb dexterity. Secondly, with the exception of the role of phylogeny, they are based upon supposition with little empirical support. That is, they are based upon *post-hoc* observations of trends within a data set and not on statistical evidence. The appropriate means of testing these theories is to incorporate a phylogenetic approach to a data set of assorted species' forelimb dexterity and to contrast this with the various correlates.

Objectives of the Present Study

There are three main aims of this thesis: 1) to derive a new dexterity rating system; 2) to assess the relative importance of different selective factors and covariates in the evolution of skilled forelimb movements in the order Carnivora, namely: relative brain and neocortical volumes, manus proportions, body size, phylogeny, arboreality and diet; and 3) to determine whether skilled forelimb movements are homologous or analogous across tetrapods.

To achieve the first two objectives of this thesis, members of the order Carnivora were examined. Although other mammalian taxa (e.g. primates, rodents) have been the focus of previous studies (Bishop 1964, Whishaw et al. 1998a), the carnivorans provide the best means of examining the evolution of skilled forelimb movements for a number of reasons. Firstly, they have a wide range of manipulative abilities, from the cheetah (*Acinonyx jubatus*) which rarely uses its forepaws in non-locomotory activities to the giant panda (*Ailuropoda melanoleuca*) which constantly grasps and manipulates food items. Secondly, they have a wider range of body types and life histories than most other mammalian orders. For example, there are some species which are almost entirely herbivorous (e.g. the giant panda) and others which are exclusively carnivorous (e.g. felids). Similarly, they span a wide range of locomotor types from fully aquatic species (e.g. sea otter (*Enhydra lutris*)), to arboreal forms (e.g. binturong (*Arctictis binturong*)) to fully 'cursorial' forms (e.g. spotted hyaena (*Crocuta crocuta*)). Thirdly, they are the focus of a myriad of comparative studies and, as a result, their phylogeny is fairly well resolved (Bininda-Edmonds et al. 1999). Thus, the phenotypic variability and resolved phylogenetic associations of the Carnivora make them an ideal group to assess the evolution of forelimb dexterity and its correlated, and possibly causal, evolution with other factors.

Since each of the various comparative methods employed differs in its statistical power and, to a lesser extent, the question it answers, a three-tiered approach was employed. Each step provides an alternative comparative method which was used to evaluate the evolution of skilled forelimb movements. These methods include: independent contrasts, phylogenetic autocorrelation and ancestral state reconstruction. The details of each are elaborated upon in subsequent chapters. Although all of the methods could have been incorporated into each chapter, they were not because of differences in the types of questions asked within each chapter. Furthermore, it provides an example of how different comparative methods can be used in concert to provide greater confidence in the conclusions reached.

As mentioned above, a significant portion of the second chapter is the development of a new dexterity rating system. The latter part of this chapter then focusses upon the first hypothesis, that relative brain size is predictive of forelimb dexterity. To test this proposed relationship, independent contrasts are used to standardise the data with respect to a known phylogeny (Bininda-Edmonds et al. 1999).

The second factor, relative digit length, is the focus of the third chapter. Through the use of independent contrasts the correlation between changes in the relative length of the digits and the dexterity index (see Chapter 3) were assessed.

Lastly, the effects of phylogeny and ecological variables were examined with respect to forelimb dexterity. Using phylogenetic autocorrelation and character mapping, the possible effects of phylogeny are quantified as well as the degree of homoplasy (i.e. parallel/convergent evolution) present in the evolution of forelimb dexterity. Independent contrasts are then employed to test the relationship between forelimb dexterity and diet (Gittleman 1986a) and locomotion (Cartmill 1985; Wood-Jones 1916). Thus, the fourth chapter examines possible selective forces involved with forelimb dexterity, rather than morphological covariates as in the previous chapters.

In the final chapter, the results of the four major comparisons will be evaluated as well as the implications of this study for the comparative examination of skilled forelimb movements and other motor behaviours. It concludes by addressing the final objective of this thesis: determining whether skilled forelimb movements are homologous or not. Through the use of character mapping, the relative importance of various descending pathways of the spinal cord are assessed. Finally, I propose a possible origin of skilled forelimb movements in tetrapods and the ramifications of this origin on our understanding of both the nervous system and the evolution of motor behaviours.

CHAPTER TWO*

A Test of the Correlated Evolution of Relative Brain Size and Forelimb Dexterity.

ABSTRACT

To test the hypothesis that brain size and forelimb dexterity are positively correlated, the relative brain size of 41 species of fissiped ('terrestrial') carnivorans (Order: Carnivora) was examined with respect to their use of the forelimbs during feeding. With the use of a newly derived dexterity index, the forelimb dexterity executed by each of the species was calculated as a single, continuous variable which was then regressed against the residuals of brain size. To account for confounding effects of phylogenetic inertia, the analysis was performed with independent contrasts analysis using a speciational model of evolutionary change (i.e. equal branch lengths). The results suggest that relative brain size and neocortex size are not correlated with the dexterity of the proximal or distal segments or a combination of the two (total forelimb dexterity). The presence of species with widely different brain sizes and similar dexterities, and vice versa, suggests that an increase in the amount of neural substrate might not be necessary for the production of finely coordinated forelimb movements. It is suggested that this outcome is representative of the plasticity of both mammalian brain size and behaviour and that variations in brain size and forelimb dexterity could be linked to disparate ecological and phylogenetic factors which act in concert to promote or constrain neural development and behaviour in different species.

* This chapter is modified from a paper published in Brain, Behaviour and Evolution 54: 167-180.

INTRODUCTION

The principle of proper mass states that the amount of neural tissue responsible for a particular function is equivalent to the amount of processing required for that function to occur (Jerison 1973). This implies that behaviours (functions) which increase in their complexity require a greater amount of tissue than those behaviours which are more simplistic. It also suggests that species which exhibit more complex behaviours possess relatively larger brains than behaviourally impoverished species (Eisenberg 1981; Jerison 1973). According to this theory, changes in the organisation of specific areas of the brain and/or their enlargement cause a 'ripple effect' such that the overall size of the brain is altered. This concept has been invoked as an explanation for the diversity of brain sizes in vertebrates and specifically in the differential execution of specific behaviours such as: social behaviour (Dunbar and Bever 1998; Pawlowski et al. 1998), feeding strategies (Gittleman 1986a; Pirlot 1981) and learning ability (Riddell 1979). One often overlooked aspect of mammalian behaviour which has been frequently associated with increases in overall brain size is forelimb or manual dexterity. An increase in the dexterity and use of the forelimbs in non-locomotory activities has been considered to be a contributing factor in the evolution of large brains in humans (Eccles 1989), predatory dinosaurs (Hopson 1977) and mammals as a whole (Nudo and Masterton 1990). In a broadly based comparative analysis, Gittleman (1986a) examined the brain size in 153 carnivoran species (Order: Carnivora) and suggested that:

> "..carnivorous species within Carnivora may have increased brain size because of a more complex foraging strategy involving selection for rapid prey detection, pursuit, capture (**especially forepaw manipulation**) and

> consumption." (Gittleman 1986a, page 34, with emphasis added).

This implies that predatory carnivorans should also possess greater manipulative ability (i.e. forepaw dexterity) based upon their larger brain size relative to insectivorous or omnivorous carnivorans.

More recently, Nudo and Masterton (1990) demonstrated that within a wide taxonomic sampling of mammals, including two carnivorans, digital dexterity is positively correlated both with the amount of corticospinal (CST) cortex and overall neocortical size. Given that cortical volume increases with increases in overall brain size (Finlay and Darlington 1995; Hofman, 1982, 1988), this supports Gittleman's (1986) finding within carnivorans.

An alternative, but less common, viewpoint is that changes to the nervous system can produce an increase in motor function without affecting overall brain size. That is to say, changes in the size or connections of specific regions of the brain can occur independently of alterations in overall brain size. This would imply that increases and decreases in forepaw use in different species may not rely upon the amount of neural substrate (i.e. overall brain size), but rather on the connectivity within and between neural structures. A lack of correlation between behavioural complexity and gross brain size is supported by a comparison between the laboratory rat (*Rattus norvegicus*) and the laboratory mouse (*Mus musculus*). Considerable evidence suggests that the rat is more complex in its behaviour than the mouse (Berridge 1990; Pellis et al. 1991; Pellis and Iwaniuk, 1999a; Poole and Fish 1975; Whishaw et al. 1998a, b), however, the relative brain size of the rat (encephalisation quotient = 0.792) is below that of the mouse (EQ = 0.808) (data from Eisenberg 1981). Similarly, solitary members of the felid genus

Panthera (i.e. the jaguar (*P. onca*), the leopard (*P. pardus*) and the tiger (*P. tigris*)) possess much larger relative brain sizes (average EQ = 1.184) than the social lion (*Panthera leo*) (EQ = 0.829), despite the apparent complexity of social group living (Schaller, 1972; data also from Eisenberg 1981). Thus, it appears to be equally plausible for forelimb dexterity not to be significantly correlated with brain size.

Most comparative analyses of brain size have suffered from a lack of direct, corroborating behavioural evidence and the brain-behaviour relationships are thus based upon a few anecdotal observations (e.g. Pirlot 1981), a crude behavioural index (e.g. Legendre et al. 1994; Legendre and Lapointe 1995) or supposition (e.g. Gittleman 1986a). The problem inherent in these types of analyses is that significant relationships between the neural substrate and a particular behaviour might be recognised when none may actually exist (i.e. a false positive or Type II error). This potential source of error can be further compounded by the inappropriateness of using species as individual data points in an interspecific comparison (Harvey and Pagel 1991). Thus, a proper assessment of the relationship between brain size and forelimb dexterity has yet to be conducted which includes : 1) a suitably diverse data set with enough species for a meaningful comparison; 2) an appropriate means of measuring the behaviour of interest; and 3) the use of modern comparative statistics that enable interspecific comparisons to be made without compromising the analysis.

To directly test the hypothesis that a large brain confers greater manipulative ability, I examined forepaw use in 45 carnivoran species, representing a wide range of ecological niches and phylogenetic histories. The species were then rated according to a newly developed dexterity index and directly compared against their brain size residuals with the use of independent contrasts analysis. If an increase in the complexity of motor output requires a relatively greater amount of neural substrate (i.e. the principle of proper mass), then there should be a significant, positive correlation between dexterity and relative brain size. If, however, increases in the complexity of motor output do not necessarily require an increase in the amount of neural substrate, then a non-significant relationship should be present. Lastly, as the amount of neocortex has been shown to increase with brain size (Finlay and Darlington 1995; Glezer et al. 1988; Hofman 1982, 1988; Nudo and Masterton 1990), relative neocortical volume was also examined with respect to forepaw dexterity in those species for which neural measurements were available.

METHODS

Species

Of the forty-five species of fissiped carnivorans (i.e. the extant Carnivora excluding the seals (phocids), sea lions (otariids) and walrus (*Odobenus rosmarus*)) observed for this study, the data on 41 of these species is presented here as these are the only species for which brain size measurements could be obtained (omitted were: Geoffroy's cat (*Leopardus geoffroyi*), sand cat (*Felis margarita*), spectacled bear (*Tremarctos ornatus*) and the forest genet (*Genetta maculata*)) (Appendix 1).

The animals were filmed at various zoological institutions with a Canon 8 mm camcorder while they were eating. Two hours of observation was deemed to be the minimum time required to include the species in the analysis. This figure is based on preliminary observations made prior to this study, as well as previously published accounts of carnivoran feeding behaviour in the wild (Van Valkenburgh 1996).

Behaviour Patterns

Previous attempts to assess the relative dexterity of non-human species have been limited because: 1) animals were pigeon-holed into specific categories which were not based on actual behaviour patterns; and 2) the studies focussed only on those movements occurring in the distal portion of the forelimb. The problem with the former limitation is two-fold. Firstly, as discussed above, the accuracy of the index is compromised by a lack of behavioural evidence to support it. Secondly, for most behaviour patterns, a categorical index is inappropriate. Behaviour patterns occur most frequently in continuums with a suite of gradations, rather than as discrete, unordered categories.

Focusing solely upon the extremities of the forelimb ignores the contribution of the whole body to the functioning of the forepaw. Studies have shown that at least some degree of control over the trunk is necessary to allow free movement of the forelimbs (Bertenthal and Von Hofsten 1998), with postural modifications being important to direct forelimb movements (Saling et al. 1996; Whishaw and Pellis 1992). Therefore, the skill with which the forepaws are used, that is dexterity, combines the flexibility of both the distal extremity (forepaw) and the proximal segments (upper forelimb, shoulder). Species differ, however, in the relative contribution of these segments. For example, in the raccoon, a high degree of forelimb dexterity largely arises from postural changes in the body and shoulder girdle flexibility, rather than from finely controlled digit and forepaw movements (Iwaniuk and Whishaw 1999).

Thus, the development of a dexterity index should incorporate information on movements occurring both proximally and distally in a continuum of values based upon observable behaviour patterns (Figure 2.1). I therefore present an index which focuses on the anatomical aspects of forelimb dexterity in mammals. In this index, a species receives a score for each of the 20+ components of the index. The scores are then tallied to produce a single score for each species. This index can also be modified with the addition of supplementary variables that might be pertinent to other taxonomic groups; a property not included in previous dexterity scales (Heffner and Masterton 1975, 1983).

Some of the characters are weighted more heavily than others and this is a reflection of the relative importance of these characters to the dexterity of forepaw use. For example, the ability to supinate/pronate the lower forelimb contributes more to the flexibility of the forepaws than does the movement of the upper forelimb, even when it occurs in more than one plane; rotation of the radius over the ulna allows the manus to adopt a greater number of postures, whereas movement of the upper forelimb away from the midline does not. It should also be noted that some characters are contingent upon others. For example, the different forms of grasping can only arise if grasping itself occurs. This is representative of the actual flexibility of forepaw movements, however, because species with a greater number of grasp types are capable of handling and manipulating a greater range of item shapes and sizes. Thus, although behavioural hierarchies exist within the index, they are representative of biological hierarchies in the organisation and variability of forepaw use and are not 'artificial' hierarchies imposed upon the behaviours by the observers. Furthermore, similar hierarchical behavioural classifications have been successfully used in other comparative studies (e.g. copulation behaviour in mammals in Dewsbury (1972)).

It should be noted, however, that the functional endpoint of the movements was not incorporated into the present index. That is, the generalised outcome, resulting from a complex suite of movements (e.g. species *x* only holds objects down with its forepaws, whereas species *y* can pick three items up in one forepaw) is not included. Attempts

Figure 2.1: A tabular representation of the index used to rate the forelimb dexterity of the 45 carnivorans. The index is divided into three major sections, body, forelimb and forepaw, which correspond to the relative contribution that each body part has in the execution of skilled forelimb movements (see text). The three forelimb dexterity scores were calculated as follows: proximal = sum of the characters under 'body' and 'forelimb'; distal = sum of the characters under 'forepaw'; and total = sum of all characters.

BODY	
1) Number of postures: one, two-three, > three	0, 1, 2

+

FORELIMB	
2) Limbs cross midline: no/yes	0, 1
3) Alternate limb-use: no/yes	0, 1
4) Upper forelimb moves in more than 1 plane: no/yes	0, 1
5) Upper forelimb rotation: no/yes	0, 1
6) Lower forelimb rotation: < 90°, 90°-135°, > 135°	0, 1, 2

+

FOREPAW	
7) Grasping occurs: no/yes	0, 1
8) Forepaw(s) pick up items: no/yes	0, 1
9) Unimanual grasping: no/yes	0, 1
10) 'Whole forepaw' grasp: no/yes	0, 1
11) D2-D3 grasp: no/yes	0, 1
12) Claw grasp: no/yes	0, 1
13) 'Other' grasp: no/yes	0, 1
14) Independent digit movements: no/yes	0, 1
15) Frequency of manipulation: none/rare, up to 60%, > 60%	0, 1, 2
16) Items swapped between forepaws: no/yes	0, 1
17) Items rotated by the forepaws: no/yes	0, 1
18) Distal digits used in manipulation: no/yes	0, 1
19) Forepaws pull away from one another: no/yes	0, 1
20) 'Other' digit/forepaw movements: no/yes	0, 1

were made to incorporate both anatomy and function of forelimb movements, but these resulted in either incomplete information on the types of forepaw use or in redundancy. Also, unlike other mammalian orders which frequently employ the forepaws to manipulate items (e.g. the rodents and the primates), carnivorans appear to be somewhat impoverished in the types of manipulation performed. The solution is to dissociate anatomy from function and treat them separately until members of other taxa (e.g. primates, rodents, marsupials) can also be incorporated.

The videotapes of 41 species were examined and scored according to this forepaw dexterity index (see Appendix 1, 2). Because proximal (body and forelimb) and distal (forepaw) dexterity could have differential relationships with brain size, the total dexterity, as well as that specific to the proximal and distal components, were analysed with respect to relative brain size and neocortical volume (see below).

Brain Size

Brain size measurements were taken directly from Gittleman (1986a). Because I tested the hypothesis that the relative size of a carnivoran's brain is an important determinant of forepaw dexterity using only a portion of Gittleman's (1986a) data set, I recalculated the allometric equation for carnivorans based on the relevant subset of species. Although the residuals calculated from this analysis might be different from those in Gittleman's (1986a) original analysis, it seemed more meaningful to use residuals specific to the subset, rather than relying upon residuals from a more inclusive analysis. Both the brain sizes and weights provided by Gittleman (1986) were used in calculating the allometric equation.

The allometric equation was calculated as having a slope of 0.605 ($\log_{10}$Brain size = 0.605$\log_{10}$Body weight - 0.711). The residuals (Appendix 1) were then used in independent contrasts analysis to compute the correlation with the dexterity index.

Brain size, however, can change in a variety of ways depending upon which structures in the brain are elaborated. To take into account the possibility of specific brain components contributing to forepaw use, rather than the brain as a whole, the relative neocortex volume was obtained for 11 species (Table 2.1) (Kamiya and Pirlot 1987; Pirlot and Jiao 1985; Rohrs 1986a ,b; Rohrs et al. 1989). The percent of neocortex out of the total brain volume was taken as a measurement of relative neocortical volume. The measurements were made independent of body size by regressing log-neocortical volume against log-body weight and using the residuals for further analysis (see also above). The allometric equation was calculated as having a slope of 0.046 ($\log_{10}$Relative neocortical volume = 0.046$\log_{10}$Body weight - 0.406). The same dexterity index values in table 1 for the 11 species and the residuals were then used in the statistical analysis.

Statistical Analysis

In recent years, it has been acknowledged that species can rarely be used as independent data points in interspecific comparisons (Harvey and Pagel 1991). Due to a shared common ancestry, species cannot be used as independent data points in conventional statistics as this is a violation of the assumption of independence. Therefore, I applied Felsenstein's (1985) method of independent contrasts analysis to the present data set. Statistically, this is the most robust and powerful comparative method currently available (Diaz-Uriarte and Garland 1996, 1998; Garland et al. 1999; Harvey and Pagel 1991; Martins and Garland 1991; Purvis et al. 1994) and it has been successfully used in other comparative analyses of neural structure size and behavioural complexity (Devoogd et al. 1993; Dunbar and Bever 1998; Iwaniuk et al. 1999a; Lefebvre et al. 1998; Pawlowski et al. 1998; Szekely et al. 1996). Briefly, this method compares

Table 2.1. Neocortical volumes for 11 carnivore species.

Species	Neocortical Volume (% of total)[a]	Source
Ailuropoda melanoleuca	0.6441	Pirlot and Jiao (1985)
Ailurus fulgens	0.5887	Kamiya and Pirlot (1987)
Chrysocyon brachyurus	0.6365	Rohrs (1986b)
Crocuta crocuta	0.6594	Rohrs et al. (1989)
Eira barbara	0.6364	Rohrs (1986a)
Hyaena brunnea	0.6182	Rohrs et al. (1989)
Mephitis mephitis	0.5030	Rohrs (1986a)
Nasua narica	0.5695	Rohrs et al. (1989)
Panthera leo	0.6789	Rohrs (1985)
Procyon lotor	0.5938	Pirlot and Jiao (1985)
Ursus americanus	0.6300	Pirlot and Jiao (1985)

[a] the amount of neocortex is shown as the percentage of the total brain volume occupied by neocortex

pair-wise values at each node of a phylogeny and divides each 'contrast' by a standard deviation derived from the branch lengths of the phylogeny to make the data independent of phylogenetic relatedness. The resulting data points are the relative differences between pairs of species (or groups of species) with each node on the phylogeny represented by a single data point.

Due to the suggestion by some (Bjorklund 1997; Price 1997; Ricklefs and Starck 1996) that these new comparative statistics are too conservative, I also analysed both data sets without correcting for relatedness using a least-squares linear regression model.

I used the composite phylogeny compiled by Bininda-Edmonds et al. (1999) as it provided resolution of the greatest number of nodes (Appendix 3). For the purposes of creating the phylogenetic tree and determining branch lengths, the domestic dog (*Canis familiaris*) was treated as equivalent to *Canis lupus* in the Bininda-Edmonds et al. (1999) phylogeny. Also, resolution in the composite phylogeny was not possible for two of the canids examined in this study, so the relationship between the maned wolf (*Chrysocyon brachyurus*) and the bush dog (*Speothos venaticus*) and the other canids was taken from Wayne et al. (1997). Resolved relationships among all the species was necessary because polytomies are unlikely to be representative of true branching in a phylogeny and the comparative analysis performed herein is more reliable without the presence of unresolved taxa (Purvis and Rambaut 1995). Furthermore, the likelihood that changes in the terminal branches would significantly affect the results of independent contrasts analysis is negligible (Price 1997).

The phylogeny, branch lengths and data set were entered into the CAIC (Comparative Analysis of Independent Contrasts) software package (Purvis and Rambaut 1995). All of the characters were treated as continuous variables and the contrasts were calculated using both a gradual and a speciational model of evolutionary change. To ensure that the data had been properly standardised (i.e. phylogenetic effects were effectively removed), the square root of the branch lengths was regressed against the contrasts calculated for each model, as suggested by Garland et al. (1993). A significant correlation was found between the branch lengths and the contrasts of the gradual model, which is indicative of improperly standardised data (Garland et al., 1993) (Table 2.2). Although the gradual model appears to remove phylogenetic effects from the proximal dexterity score effectively (Table 2.2), the lack of standardisation of the independent variable (relative brain size) in the gradual model meant that only the contrasts calculated for the speciational model could be used in further analyses. The raw data and contrasts were subsequently tested for normality using Shapiro-Wilk W-tests. The raw data for the total ($W = 0.87$, $P < 0.01$) and distal ($W = 0.89$, $P < 0.01$) dexterity scores and the contrasts of relative brain size ($W = 0.80$, $P < 0.01$) were not normally distributed. Transformations (log, square-root, cube-root) of the raw dexterity scores did not result in normalisation of the data. Therefore, both least-squares linear regressions and Spearman correlations were performed on the raw data. Square-root transformation of the brain size contrasts did result in a normal distribution ($W = 0.96$, $P = 0.29$) and therefore, both least-squares and reduced major axis regression through the origin (Garland et al., 1992) was performed on the contrasts data. Given that the total dexterity score is a combination of both the proximal and distal dexterity scores, a multiple regression analysis forced through the origin was also implemented.

The neocortical volume data was entered into the CAIC program in the same fashion as the total brain size residuals (see above) and using the same phylogeny from Bininda-Edmonds et al. (1999) (Appendix 3). Again, the data was treated as continuous

Table 2.2. The results of the regression analyses of the absolute value of the independent contrasts against the square root of branch lengths for two models of evolutionary change: gradual ('Unequal') and speciational ('Equal').

Branch lengths			*F*[a]	*p*[b]
Unequal				
	Brain size		8.28	0.01
		Total	4.25	0.05
		Proximal	0.86	0.36
		Distal	4.34	0.04
	Neocortical volume		1.77	0.22
		Total	0.79	0.39
		Proximal	0.48	0.51
		Distal	0.91	0.37
Equal				
	Brain size		0.05	0.83
		Total	0.09	0.76
		Proximal	0.02	0.90
		Distal	2.94×10^{-7}	0.99
	Neocortical volume		3.83	0.09
		Total	1.38	0.27
		Proximal	1.58	0.24
		Distal	1.44	0.26

[a] degrees of freedom for brain size contrasts = 1, 38 and for isocortical volume contrasts = 1, 8.

[b] note that a significant result is indicative of improperly standardized data

and the contrasts were calculated using both models of evolutionary change. Both models resulted in properly standardised data (Table 2.2), but for the sake of consistency with the brain size contrasts, only the speciational, or equal branch length, model was used in further analysis. Shapiro-Wilk W-tests for normality indicated that all of the raw data was normally distributed and that, with the exception of the neocortical volume residuals($W = 0.66$, $P < 0.01$), the contrasts were also normally distributed. Cube-root transformation of the neocortical volume contrasts resulted in a normal distribution ($W = 0.86$, $P = 0.08$) and was used in subsequent analyses. Both least squares and reduced major axis regression models were then implemented to test for significance. Multiple regression of the proximal and distal dexterity scores was also used as above.

Lastly, it should be noted that although only simple linear relationships are shown, similar results were obtained with polynomial and exponential models.

RESULTS

No significant relationship was found between the raw scores of brain size and the three dexterity measurements using a least-squares linear regression (Table 2.3). Calculation of Spearman correlations provided similar results ($Z_{total} = 0.57$, d.f. = 40, $P = 0.57$; $Z_{distal} = 0.85$, d.f. = 40, $P = 0.40$; $Z_{proximal} = -0.03$, d.f. = 40, $P = 0.97$). The plots of the dexterity contrasts against the brain size contrasts showed a high amount of variability inconsistent with a significant correlation (Figure 2.2). The regression lines, both least squares and reduced major axis, were not significant for any of the dexterity scores (Table 2.3). Multiple regression analysis of the proximal ($F = 4 \times 10^{-6}$, d.f. = 1, 38, $P = 0.99$) and distal contrasts ($F = 0.02$, d.f. = 1, 38, p = 0.88) against the brain size contrasts was also non-significant. Thus, there does not appear to be a significant

Table 2.3. The correlation coefficients (r^2's) and slopes calculated from the regression analysis of the three dexterity measurements against relative brain size.

	Dexterity score	Raw [a]	Least squares [b]	Reduced major axis
Brain size	Proximal	-1.33 (0.003) [c]	-0.62 (0.010)	-59.97 (0.010)
	Distal	2.75 (0.004)	-0.80 (0.016)	-51.59 (0.016)
	Total	1.41 (0.004)	-1.18 (0.006)	-214.73 (0.006)
Neocortical volume	Proximal	-6.85 (0.002)	0.79 (0.023)	34.84 (0.023)
	Distal	-20.72 (0.008)	1.00 (0.013)	80.08 (0.013)
	Total	-28.93 (0.006)	1.61 (0.013)	126.02 (0.013)

[a] data without phylogenetic effects removed (brain size d.f. = 1, 39; neocortical volume d.f. = 1, 9). None of the regression lines were significant ($p > 0.10$).

[b] both the 'Least squares' and 'Reduced major axis' analyses utilized independent contrasts rather than raw data (brain size d.f. = 1, 38; neocortical volume d.f. = 1, 8). None of the regression lines were significant ($p > 0.10$)

[c] slope is shown outside of the brackets and the correlation coefficients inside the brackets

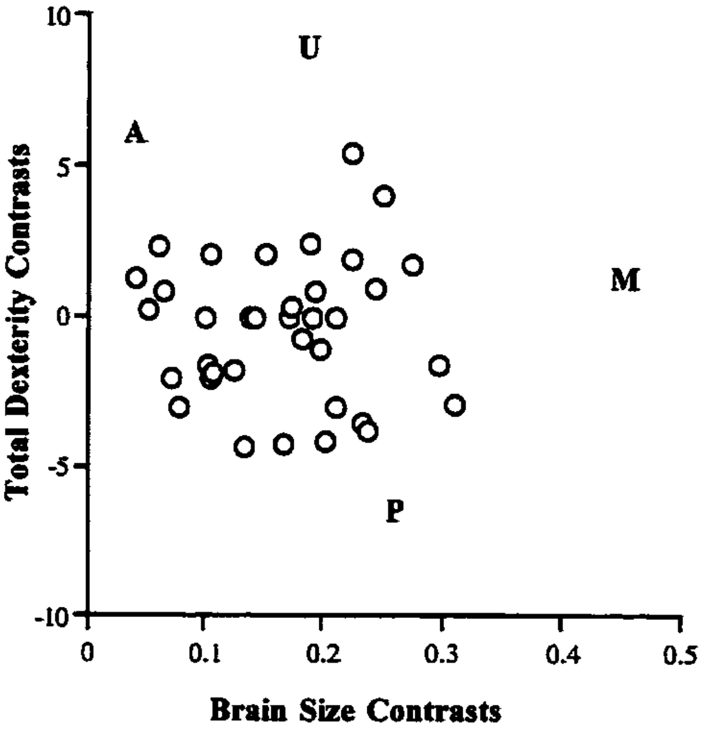
relationship between overall brain size and forepaw dexterity in carnivorans.

No significant relationship was found in the raw comparison of neocortex size and the three dexterity measures (Table 2.3). An *x*-*y* plot of the contrasts revealed that there was considerable variation in the relative size of the neocortex and all three dexterity measures (Figure 2.3), but that none of the correlations were significant (Table 2.3). Multiple regression of the proximal ($F = 1.07$, d.f. = 1, 8, $P = 0.33$) and distal dexterity ($F = 1.21$, d.f. = 1, 8, $P = 0.30$) contrasts against the neocortex contrasts was also non-significant.

Outliers, those data points which have conspicuously large residuals, often provide insight into species differences as they represent exceptions to the general pattern. In the present analysis, four data points had contrast values which were considerably larger and smaller than the rest of the data. Three of these points are outliers on the y-axis and represent behavioural differences: the cheetah (*Acinonyx jubatus*)-Felidae contrast; the brown bear (*Ursus arctos*)-polar bear (*Ursus maritimus*) contrast; and the masked palm civet (*Paguma larvata*)-binturong (*Arctictis binturong*) contrast (Figure 2.2). The remaining data point is an outlier on the x-axis, however, and represents a neural difference: the contrast between the striped skunk (*Mephitis mephitis*) and the Lutrinae (otter) lineage (Figure 2.2). With respect to the regression analyses of relative neocortical volume, only one contrast appears to be disjunct from the rest of the data: the contrast between the striped skunk and the tayra (*Eira barbara*) (Figure 2.3).

Figure 2.2: Scatter plots of the contrasts calculated for the brain size residuals and **a)** total dexterity and **b)** proximal (open circles) and distal (closed circles) dexterity. Outliers are indicated as follows: '**A**' - the contrasts between the cheetah (*Acinonyx jubatus*) and the rest of the Felidae; '**M**' - the contrasts between the striped skunk (*Mephitis mephitis*) and the Lutrinae; '**P**' - the contrasts between the masked palm civet (*Paguma larvata*) and the binturong (*Arctictis binturong*); and '**U**' - the contrasts between the brown bear (*Ursus arctos*) and the polar bear (*Ursus maritimus*). The subscripts '$_p$' and '$_d$' refer to proximal and distal dexterity scores respectively.

a)


10
5
0
-5
-10
Total Dexterity Contrasts
U
A
M
P
0
0.1
0.2
0.3
0.4
0.5
Brain Size Contrasts

b)

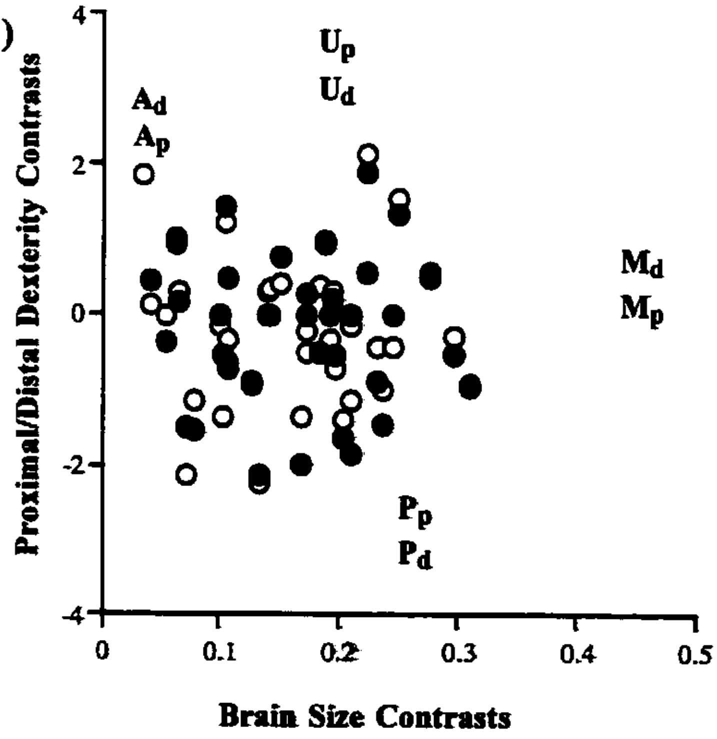
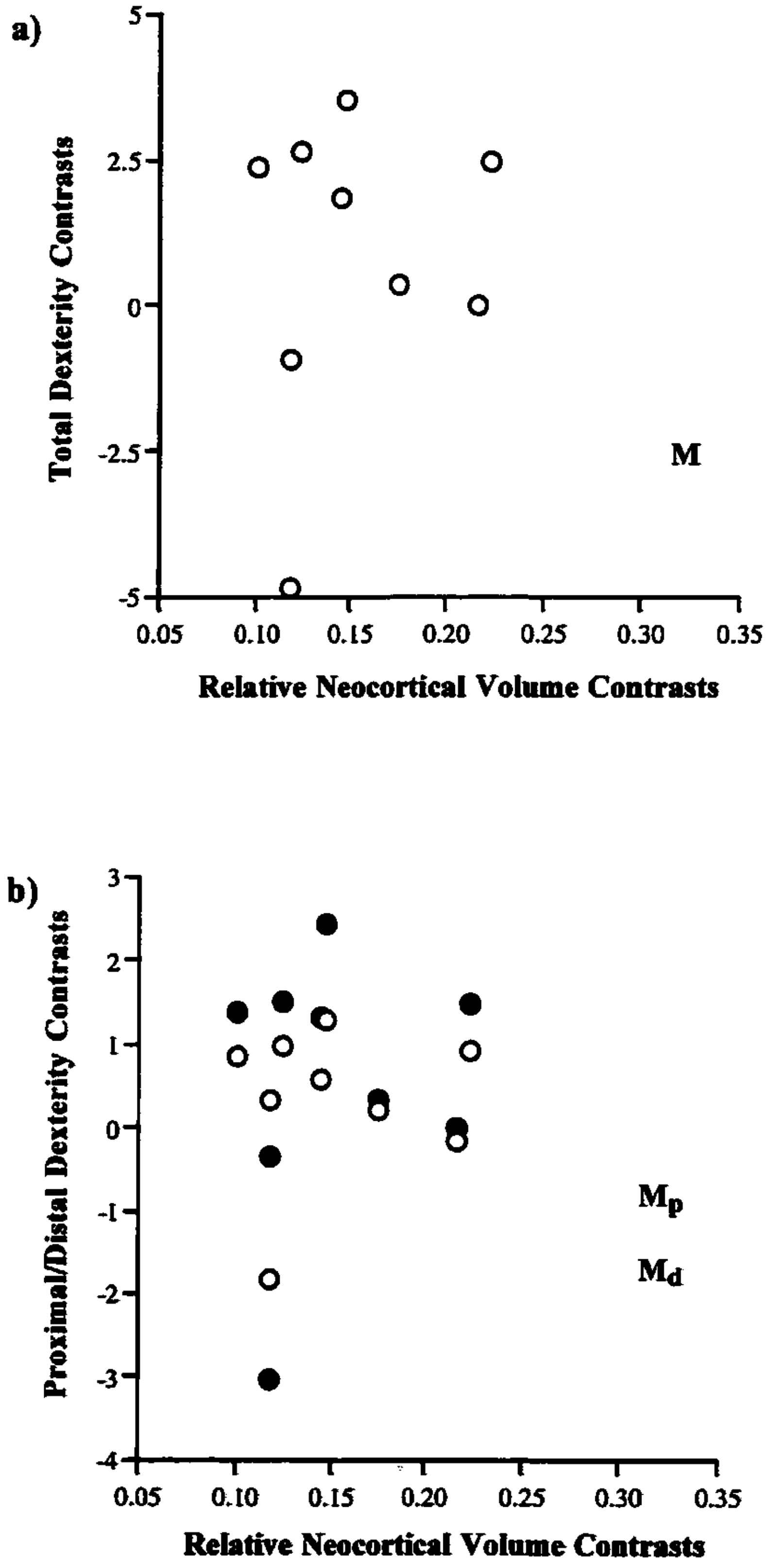

4
2
0
-2
-4
Proximal/Distal Dexterity Contrasts
U_p
U_d
A_d
A_p
M_d
M_p
P_p
P_d
0
0.1
0.2
0.3
0.4
0.5
Brain Size Contrasts

Figure 2.3: Scatter plots of the contrasts calculated for the neocortical volume residuals and **a)** total dexterity and **b)** proximal (open circles) and distal (closed circles) dexterity. One outlier, the contrast between the striped skunk (*Mephitis mephitis*) and the tayra (*Eira barbara*), is indicated by a 'M'. The subscripts '$_p$' and '$_d$' refer to proximal and distal dexterity scores respectively.


a)
5
2.5
0
-2.5
-5
Total Dexterity Contrasts
0.05
0.10
0.15
0.20
0.25
0.30
0.35
Relative Neocortical Volume Contrasts
M
b)
3
2
1
0
-1
-2
-3
-4
Proximal/Distal Dexterity Contrasts
0.05
0.10
0.15
0.20
0.25
0.30
0.35
Relative Neocortical Volume Contrasts
Mp
Md

DISCUSSION

The lack of a significant correlation between both overall brain size and neocortical volume and forelimb dexterity is a clear rejection of the principle of proper mass. This, in turn, suggests that alterations in forelimb dexterity can be achieved through more subtle means, such as connectivity between neural structures, rather than through gross changes in the morphology of the central nervous system. Due to the specificity of the present data set, however, a number of caveats must be taken into account in the interpretation of the results.

Differences in Behaviour and Brain Size

As mentioned previously, the examination of outliers can often be instructive in elucidating the relationships observed in a correlational analysis. In all of the comparisons with overall brain size, the contrast with the largest residual was that between the cheetah and the rest of the Felidae (Figure 2.2). Unlike most of the other felids, the cheetah rarely uses its forepaws to manipulate food items (pers. obs.; Eaton 1974; Van Valkenburgh 1996). Even the use of forepaws during prey capture is significantly less in cheetahs than other felids. The dewclaws are used to snag prey, and subsequent killing does not require the forepaws to be used (Eaton 1974; Leyhausen 1979). If this is compared with the majority of the Felidae, the contrast in forepaw-use is considerable. Most of the felids examined not only uses their forepaws to capture and subdue prey (Leyhausen 1979), but also in the manipulation of food items (pers. obs.). This behavioural difference results in the large residuals for the cheetah-Felidae contrast in the x-y plots (Figure 2.2).

A second common outlier to the analyses of overall brain size was the contrast between the brown bear and the polar bear. In a similar fashion to the cheetah-Felidae contrast, this contrast also relates to profound differences in forepaw-use between the two species. The polar bear rarely uses its forepaws to manipulate food items. Instead, the polar bear simply holds food down as it is sheared and pulled apart by movements of the head and neck. The brown bear, on the other hand, almost always uses its forepaws to reach for, grasp and manipulate food items. Thus, despite similar brain sizes, their forepaw-use is considerably different and the residual of the contrast between these species is high.

The third common outlier is the contrast between the masked palm civet and the binturong. Again, this relates to profound behavioural differences between these two viverrids. The palm civet was not observed using its forepaws in any way during feeding, although it has been observed to use the forepaws in prey capture (Eisenberg and Leyhausen 1972; Wemmer 1977). The binturong, in contrast, used its forepaws to grasp and manipulate most food items. Thus, the two species exhibited divergent forepaw use in a similar fashion to the cheetah-Felidae and brown bear-polar bear contrasts.

All of the above outliers concern behavioural differences more than neural ones. Only one outlier occurred in the brain size contrasts; between the striped skunk and the base of the Lutrinae branch (see Appendix 3). The uniqueness of the skunks (Mephitinae) has been recognised frequently in the literature based upon molecular (Dragoo and Honeycutt 1997; Ledje and Arnason 1996; Vrana et al. 1994), osteological (Wozencraft 1989) and neural (Radinsky 1973; Rohrs 1986a) differences between the mephitines (*Mephitis*, *Conepatus*, *Spilogale* and *Mydaus*) and the other mustelids. The distinctiveness of the Mephitinae is also reflected in the contrast between the only mephitine examined (the striped skunk) and the Lutrinae being an outlier. The striped skunk possesses the smallest relative brain size of all the species examined (residual = -

0.319). It is especially low compared to the mustelids (Mustelinae + Lutrinae) which all possess quite large brains (Mustelidae average = 0.115). This is also supported by Rohrs' (1986a) analysis of mustelid encephalisation in which the striped skunk was well below the regression line, although the common (*Conepatus chinga*) and Patagonian (*C. humboldti*) hog-nosed skunks did have slightly positive residuals. In addition to this apparent reduction in overall brain size, there is also a reduction in the relative size of the neocortex, such that the striped skunk also has the lowest neocortical volume relative to its body size. It is this drastic reduction in neocortical volume that resulted in the contrast between the striped skunk and the tayra (which has a relatively large neocortical volume) lying apart from the rest of the neocortex data (Figure 2.3). The ultimate reason for this apparent reduction in brain size that has occurred within the Mephitinae is unclear due to the restricted nature of the present study. One possibility, however, is that it has resulted from changes to their body size rather than their brain size. The skunks' ability to deter most predators (the notable exception being some raptors (Wade-Smith and Verts 1982)) and their omnivorous habits might allow them to increase their body size without the compromising effects of lack of manoeuvrability which most other carnivorans would find essential in both fleeing from predators and capturing prey. Thus, it might not be a reduction of brain size, but rather a release of the constraints acting upon body size that results in the low relative brain size for the striped skunk.

Brain Size and Forepaw Use

Although the principle of proper mass does appear to be applicable to some behaviours (e.g. Devoogd et al. 1993; Dunbar and Bever 1998; Meier 1983; Pawlowski et al. 1998; Szekely et al. 1996), it does not appear to apply to the relationship between brain size and forepaw dexterity in carnivorans. Thus, the alternative hypothesis, that it might not be necessary for a species to have a relatively greater amount of neural substrate to perform complex behaviours, appears to be supported by the absence of a significant relationship between brain size and forelimb dexterity. This, in turn, suggests that the execution of finely coordinated or complicated forelimb movements can be achieved by alterations in the connectivity between limb segments and the nervous system or connections within the nervous system itself, a concept also proposed by Aboitiz (1996) and demonstrated by Nudo and Masterton (1990). If, for instance, it becomes necessary for a given species to execute independent digit movements, this could be accomplished by increasing the relative amount of peripheral innervation to the digits themselves (e.g. increase number of branching fibres from the spinal cord) without requiring any additional neural tissue in the central nervous system itself. One such example from the Carnivora is the raccoon. The raccoon's forelimb dexterity is quite high compared to other carnivorans (see Appendix 1 and Iwaniuk and Whishaw 1999), but its brain size is similar to that predicted by body size (residual = 0.019). The raccoon does, however, possess long corticospinal tract fibres that penetrate deep into the ventral horn of the spinal cord (lamina VIII-IX) (Petras and Lehman 1966). This suggests that the innervation of motoneurons in the forelimb of the raccoon has been increased without an appreciable change in the overall size of the CNS. Although the precise role that the corticospinal tract plays in the execution of forelimb and forepaw movements is unclear (Iwaniuk et al. 1999a), it would appear that the extension of these innervations is related to the wealth of forelimb and forepaw flexibility in the raccoon. Other evidence supporting this alternative theory is the presence of a diverse array of collateral projections in tectospinal and reticulospinal neurons in the cat (*Felis domesticus*) that penetrate to variable laminar depths without any apparent change in the overall size of the neurons (Shinoda et al. 1996). Thus, it would appear that extensive changes in both connectivity and size of the peripheral nervous system can be related to forepaw use and this need not necessarily result in alterations in the overall size of the central neural substrate.

The lack of a significant relationship between brain size and forelimb dexterity is also not surprising in that the size of the brain is subject to a variety of selective forces. Diet (Gittleman 1986a; Pirlot 1981; Pirlot and Stephan 1970), locomotion (Pirlot 1981) and phylogeny (Gittleman 1986a; Martin and Harvey 1985; Pagel and Harvey 1988) can all exert effects which can constrain or promote brain development. Variation in other more specific factors such as basal metabolic rate (McNab and Eisenberg 1989), diving depth (Worthy and Hickie 1986), gestation length (Marino 1997) and reproductive effort (Meier 1983) do not, however, exhibit significant correlations with brain size. It might be that brain size is subject to such a myriad of compromises within an organism that correlations with fine levels of behaviour, such as forelimb dexterity, become obliterated in large, interspecific comparisons by gross behavioural differences (e.g. diet, locomotion). Although this could be viewed as a 'negative' outcome, I propose that this is representative of the plasticity of both the nervous system and behaviour. If, for example, two species possess different relative brain sizes yet feed on the same food items in similar habitats, they might evolve similar means of finding food and feeding (also see the outliers described above). This is exemplified by the Asiatic black bear (*Ursus thibetanus*) and the American black bear (*Ursus americanus*), two species which have different brain sizes (residuals of 0.180 and -0.076 respectively), yet feed on similar foods (Herrero 1972; Holcroft and Herrero 1991; Schaller et al. 1989) and share similar modes of foraging and feeding (both possess total forelimb dexterity indices of 20).

Conversely, it is equally plausible that if the two species possessed similar brain sizes, they could evolve disparate foraging and feeding strategies (also see the outliers described above). There are a number of examples of this in the present data set, but the most profound difference is that between the cheetah and the binturong. The relative brain sizes of these two species are similar (-0.129 and -0.135 respectively), but they maintain vastly different foraging styles (terrestrial predator and arboreal opportunist), diets (Eaton 1974; Lekagul and McNeely 1977) and forelimb dexterities (1 and 14 respectively). Thus, both brain and behaviour can evolve separately depending upon the interactions occurring between a suite of ecological and phylogenetic factors and the nervous system (see also Aboitiz 1996).

Brain Size and Behaviour

Although the present study could be taken as evidence discounting the relationship between brain size and forelimb dexterity, it is important to note two key points. Firstly, it is possible that the lack of a significant correlation between brain size and forelimb dexterity is limited only to carnivorans. In a broader-based taxonomic sampling, or in a comparison within other taxa (e.g. Marsupialia, Primates, Rodentia), a significant relationship might occur. This was, in fact, demonstrated by Nudo and Masterton (1990), but their analysis was compromised by neglecting to appropriately control for phylogenetic effects (see below and Iwaniuk et al., 1999) and the implementation of crude behavioural measures (Iwaniuk et al. 1998; Iwaniuk and Whishaw 1999; Iwaniuk et al. 1999a). Thus, until such time as a greater number of species are examined and phylogeny is accounted for, the present findings should be considered applicable only to the Carnivora.

Secondly, the lack of a significant relationship between overall brain size and neocortical volume and forelimb dexterity does not exclude the possibility that the size of other neural structures could be significantly correlated with forelimb dexterity. It is certainly plausible that motor cortex, frontal cortex or some other partitioning of brain morphology might be significantly correlated with forelimb dexterity. Based upon recent observations of hand use in humans (*Homo sapiens*) and bonobos (*Pan paniscus*) (Christel 1993; Christel et al. 1998), I find this to be unlikely. Christel (1993) and colleagues (Christel et al. 1998) clearly demonstrate that although humans and bonobos use their hands at different frequencies, they are capable of performing remarkably similar grasp types, including tip-to-tip grips. Despite these similarities, the brain sizes of the two species are vastly different (an EQ between 2 and 3 for *P. paniscus* and between 7 and 8 for *H. sapiens* from Eisenberg 1981) as is the cerebellum (8.71 and 21.75 respectively) and the neocortex (71.73 and 196.41 respectively) (both from Eccles 1989). Their corticospinal projections, however, are comparable as the fibres project as far down as the coccyx and penetrate as deep as lamina X in both species (Kuypers 1981; Petras 1968). Thus, not only are carnivoran species with different brain sizes capable of performing similar movements, but it would appear that the same phenomenon exists in hominoids.

The importance that phylogeny can play in the determination of brain size cannot, however, be discounted. In a comparative study of olfactory bulb size in carnivorans, Gittleman's (1991) results from autocorrelation indicate that brain size is highly correlated with the taxonomic rank of a species. Thus, there is some phylogenetic inertia acting upon brain size in carnivorans, such that species within a genus are likely to share similar brain size measurements. These, and other findings (Pagel and Harvey 1988), suggest that the inherited component of brain size in mammals can be considerable, although it only appears to be significant at certain taxonomic levels. Thus, it is surprising that contemporary investigations into brain size and behaviour relationships have only recently begun using modern comparative statistics (e.g. Devoogd et al. 1993; Dunbar and Bever 1998; Iwaniuk et al. 1999a; Lefebvre et al. 1998; Pawlowski et al. 1998; Szekely et al. 1996). Although non-significant results were present in both the analysis of 'raw' data and the independent contrasts, the importance that phylogeny can play in the evolution of differential brain size cannot be ignored. Particularly in taxa such as the Carnivora where body morphology and diet are constrained to relatively few 'ecomorphs' in some families, but can be diverse in others, it behoves comparative researchers to take phylogenetic relatedness into account. Failure to do so can not only result in confounded conclusions, but also result in the definition of causal relationships that do not exist (Iwaniuk et al. 1999a).

CHAPTER THREE

Are Long Digits Correlated With High Forepaw Dexterity?*

ABSTRACT

The relationship between manus proportions and forepaw dexterity in 32 species of carnivorans (Carnivora) was examined. Both the regression analysis of 'raw' data and independent contrasts revealed no significant correlation between the metacarpal-phalanx (MCP) ratio and forepaw dexterity. Together, these results suggest that the morphological basis for variations in manipulative behaviour may be quite complex. Other morphological features, such as manus and carpal shape and myology, may play a critical role in forepaw dexterity, but are not manifested as changes in manus proportions. Behavioural observations also indicate that manus proportions may be more closely correlated with locomotion than with non-locomotory forepaw behaviours.

* This chapter is modified from a paper submitted for publication to the Journal of Mammalogy.

INTRODUCTION

The gross morphology of the mammalian manus has been used as an indicator of manual dexterity in a range of primate (Napier 1961) and non-primate (Heffner and Masterton 1975, 1983; Nudo and Masterton 1990) species. Generally, it is assumed that relatively longer digits permit better grasping ability and higher manual dexterity (Napier 1980). Manus morphology, however, is also constrained by locomotor demands such that interspecific variation reflects substrate preferences and/or patterns of locomotion (Szalay 1994). Gross manus morphology is therefore a trade-off between the requirements of body support and other manual activities, such as grasping and manipulating food items. Consequently, manus morphology may not readily predict manual dexterity. For example, the manus of the Canadian lynx (*Lynx canadensis*) is quite broad with relatively long phalanges relative to their metacarpals (Iwaniuk et al. 1999b; Van Valkenburgh 1985). According to Napier's (1980) assumption, the lynx should exhibit relatively good manipulatory skills compared to felids with shorter phalanges (e.g. cougar (*Puma concolor*)). Contrary to Napier's (1980) theory, however, the lynx has poor dexterity whereas the cougar has good manipulative skills (Appendix 1).

It is, however, possible that manus proportions may be related to forepaw dexterity, but that such a relationship may be masked by locomotor demands. Therefore, a comparative test is required to determine the degree to which manus morphology can predict actual manipulative abilities. If Napier's (1980) theory is correct for Carnivora, then I expect that there will be a significant relationship between manus proportions and forepaw dexterity.

METHODS

The manus proportions of 32 species of carnivorans were taken from published sources (Davis 1964; Van Valkenburgh 1985, 1987; Iwaniuk et al. in press) and previously unpublished data obtained from the Provincial Museum of Alberta (Edmonton, Alberta, Canada) (Appendix 1). In all instances, the third metacarpal and third proximal phalanx were measured in adult museum specimens with callipers. Manus proportions were then calculated by dividing the length of the third metacarpal by the length of the third proximal phalanx to yield a metacarpal-phalanx (MCP) ratio. Higher MCP ratios indicate relatively short digits whereas lower MCP ratios indicate relatively long digits. Although other ratios are used in the literature (e.g. Lemelin 1999; Lemelin and Grafton 1998), this ratio was specifically chosen because of its use in extrapolating the behaviour of fossil species (Van Valkenburgh 1985, 1987) as well as providing a basic measurement of the size of the digits relative to the palm. As there exists the possibility that the MCP ratio is correlated with body size (Albrecht et al. 1993), it was first regressed against average species body weights (Appendix 1) using both 'raw' data and independent contrasts (see below).

The behavioural measurement employed was the distal dexterity index discussed in the previous chapter (Appendices 1 and 2). Since relatively longer digits should result in better grasping and manipulatory abilities (Napier 1980), I predicted that if a significant relationship between MCP ratio and forepaw dexterity is present, then it should be negative.

Two types of statistical analysis were employed to test Napier's (1980) theory. Firstly, each species was treated as an independent data point and linear least-squares regression was applied. The MCP ratio was log-transformed to achieve a normal distribution and the distal dexterity scores were regressed against it. Use of this method, however, violates the statistical assumptions of independence because all of the species share a common ancestry (see previous chapter and Harvey and Pagel 1991). Therefore, independent contrasts were also used to analyse the relationship between manus proportions and forepaw dexterity. Again, the phylogeny and branch lengths presented in Bininda-Edmonds et al. (1999) were employed (Appendix 3).

In the independent contrasts approach, contrasts are made at each node throughout a phylogeny and standardised according to their branch lengths. These independent contrasts were calculated with the CAIC computer package (Purvis and Rambaut 1995). Both a speciational (i.e. equal branch lengths) and a gradual (i.e. unequal branch lengths) model were employed to ensure that the contrasts were properly standardised (Garland et al. 1993). Analysis of the branch lengths and the contrasts indicated that unequal branch lengths did not adequately standardise the dexterity contrasts ($F = 4.39$, d.f. = 1, 29, $P = 0.04$), but that equal branch length contrasts were properly standardised ($F = 3.18$, d.f. = 1, 29, $P = 0.09$). The contrasts from the speciational model were then checked for normality using Shapiro-Wilk W-tests (JMPIN v.3.2.1, SAS Institute) and regressed through the origin (Garland et al. 1992).

RESULTS

Regression analysis of both the 'raw' MCP ratios and standardised, normalised contrasts against body size were not significant (raw: $F = 0.23$, d.f. = 1, 30, $P = 0.64$; independent contrasts: $F = 1.17$, d.f. = 1, 29, $P = 0.29$). Therefore, the MCP ratios were directly compared against forepaw dexterity.

Regression analysis of the 'raw' data did not result in a significant relationship between the MCP ratio and forepaw dexterity ($F = 2.97$, d.f. = 1, 30, $P = 0.10$) (Figure 3.1a). The presence of a significant outlier on the *x*-axis, the maned wolf, may have contributed to this lack of significance, so the analysis was performed again with the omission of this outlier. The omission of the maned wolf did not, however, result in significance ($F = 2.03$, d.f. = 1, 29, $P = 0.17$). Similar results were obtained with the application of various non-linear regression models (e.g. polynomial, exponential).

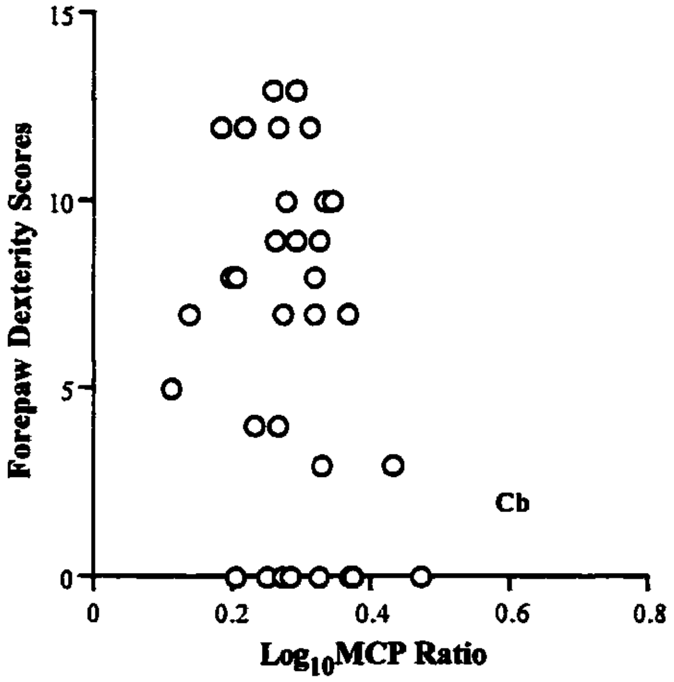
The independent contrasts of MCP ratio were not normally distributed (Shapiro-Wilk $P < 0.05$), but a cube-root transformation was successful in normalising their distribution (Shapiro-Wilk $P > 0.05$). Regression analysis of the normalised contrasts was not significant when all contrasts were included ($F = 0.08$, d.f. = 1, 30, $P = 0.77$) (Figure 3.1b). The presence of two outliers, the contrasts between the brown bear and the polar bear and the maned wolf and bush dog (*Speothos venaticus*), may have contributed to the lack of effect and were therefore removed and the analysis performed again. The removal of the *Ursus* contrast ($F = 0.15$, d.f. = 1, 29, $P = 0.71$), the *Chrysocyon-Speothos* contrast ($F = 0.64$, d.f. = 1, 29, $P = 0.43$) or both of them ($F = 1.51$, d.f. = 1, 28, $P = 0.23$) did not, however, result in significance. As in the analysis of the 'raw' data, similar results were found with the use of non-linear regression models (e.g. polynomial, exponential).

DISCUSSION

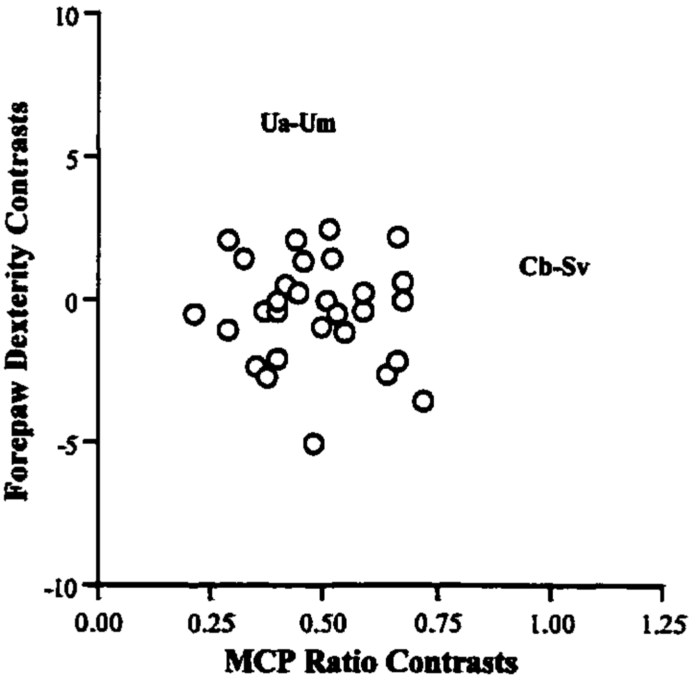
Contrary to Napier's (1980) theory that manus proportions and forepaw dexterity are correlated, the present findings indicate that a significant relationship between the MCP ratio and forepaw dexterity does not exist in terrestrial carnivorans. Although there are implicit caveats in the use of comparative methods (Harvey and Pagel

Figure 3.1: Scatter plots of the distal (or forepaw) dexterity scores against the metacarpal-phalanx (MCP) ratio: **a)** 'raw' data with species as independent data points and **b)** independent contrasts. The outliers on each graph are as follows: **'Cb'** - the maned wolf (*Chrysocyon brachyurus*); **'Cb-Sv'** - the contrast between the maned wolf and the bush dog (*Speothos venaticus*); and **'Ua-Um'** - the contrast between the brown bear (*Ursus arctos*) and the polar bear (*Ursus maritimus*). Note that the removal of these outliers did not affect the significance of the results (see text).

a)


15
10
5
0
Forepaw Dexterity Scores
Cb
0
0.2
0.4
0.6
0.8
Log_{10}MCP Ratio

b)


10
5
0
-5
-10
Forepaw Dexterity Contrasts
Ua-Um
Cb-Sv
0.00
0.25
0.50
0.75
1.00
1.25
MCP Ratio Contrasts

1991; Pagel 1993) and the method used to create the carnivoran 'super-tree' is somewhat controversial (see Chapter 5 and Bininda-Edmonds and Bryant 1998; Bininda-Edmonds et al. 1999), the consistency of the results suggests that the observed pattern is real.

The lack of association between the MCP ratio and forepaw dexterity is also apparent in a cursory examination of the data set. For example, within *Panthera*, the snow leopard (*P. uncia*) has the lowest MCP ratio and the lowest forepaw dexterity (Appendix 1). The jaguar (*P. onca*) has the next lowest MCP ratio, but has the highest forepaw dexterity of the five species. The remaining species have varying MCP ratios all above that of the jaguar and have similar forepaw dexterity scores to one another. This reinforces the conclusion that changes in the MCP ratio are not consistently related to forepaw dexterity.

One possible explanation for this non-significant relationship is that a simple ratio of metacarpal to proximal phalanx length is not informative enough about the shape of the manus. Although the manus is a functionally integrated unit, some spatial independence is likely to be present between its constituent bones. The morphology of these independent components could therefore be altered with little modification to the gross morphology of the manus itself. Similarly, the dexterity of the manus could be modified by relatively minor changes in the structure of many of the components. Thus, manus morphology may be related to forepaw dexterity at some level, but the variations in manus morphology responsible for significant functional differences may be too subtle to be detected by a simple ratio. A possible solution to this problem would be to incorporate a multivariate approach, similar to that used in Jouffroy et al.'s (1993) biometrical study of primate hands.

Similarly, the relative proportions of the metacarpals and phalanges may be relatively unimportant in the execution of different manipulative behaviours, compared to the arrangement of the carpal bones. The curvature of the carpal bones can yield marked variations in the degree of flexibility present in the wrist (Yalden 1970). This flexibility in the wrist could then be translated into better manipulatory skills. It is difficult, however, to develop a suitable means of examining carpal morphology because the three dimensional shape of each bone can have a significant effect upon the mobility of the joint. One possible means of alleviating this problem would be an eigenshape (MacLeod and Rose 1993) or thin-plate spline approach (Swiderski 1993) for each bone and then a multivariate analysis of all of the bones.

A third possibility is that myological differences may be more important to forepaw dexterity than osteological differences. Although this is in part related to changes to osteological morphology, the relative size of muscle groups and minor variations in their origins and insertions may result in functional differences without grossly affecting bone morphology. Thus, if some aspects of manus morphology are conserved through evolution (as suggested by Szalay 1994), then a possible means of increasing forepaw dexterity may be myological changes (Landsmeer 1993). For example, the American black bear and the polar bear differ in their forepaw dexterity, but have similar MCP ratios (Appendix 1). Species differences are, however, present in their myology, such as the size of the *supinator brevis* and number of tendons extending from the *flexor sublimis digitorum* (Windle and Parsons 1897). Muscle differences also appear to lead to variations in the motor abilities in primates (Landsmeer 1993), so it is possible that such myological differences could be partially responsible for dexterity differences in carnivorans. An investigation of the comparative myology of the forepaws of carnivorans is required to properly address the issue of muscle morphology.

Apart from the roles of other aspects of forepaw morphology in the execution of complex forepaw movements, there is a more direct rationale for the lack of correlation between relatively long digits and forepaw dexterity. Relatively short or long digits may be important for behaviours other than food manipulation. For example, all of the species which are adapted to movement over snow (i.e. wolverine (*Gulo gulo*), lynx, snow leopard and polar bear) possess smaller MCP ratios (Appendix 1) than the average (2.023 ± 0.500). These same species also have relatively poor forepaw dexterity. Thus, it would appear that relatively longer digits can be advantageous for behaviours other than object manipulation without conferring any significant increase in their ability to manipulate objects. Conversely, the relatively short digits of the striped skunk, which are presumably an adaptation to its frequent digging habits, do not appear to hinder their ability to manipulate food items. In fact, the striped skunk uses its long claws as a functional extension of its digits in manipulating food (pers. obs.) in a similar fashion to that reported for tree kangaroos (Iwaniuk et al. 1998). Lastly, similar phenomena are also known to occur in rodents. For example, although the red (*Tamiasciurus hudsonicus*) and Eastern grey squirrels (*Sciurus carolinensis*) have long digits, both species utilise their reduced pollices in handling food items more than their other digits (Whishaw et al. 1998). Thus, the proportions of the manus, and their relationship to forepaw dexterity, appears to be contingent upon the specific behaviours performed by individual species and the trade-off between locomotor and feeding requirements.

The findings presented herein demonstrate that the morphological basis of varying manipulative capabilities is complex and is therefore unlikely to be resolved by simplistic measurements. The observation of poor forepaw dexterity in both carnivorans and some non-carnivorans, despite possessing relatively long digits (e.g. some carnivorans, squirrels), further supports the apparent lack of relationship between forepaw dexterity and manus morphology. That is, the evidence does not appear to support Napier's (1980) theory that forepaw dexterity necessarily increases with relative digit length. Future investigations into the relationship between forepaw dexterity and manus morphology should therefore attempt to examine manus morphology from a multivariate or finer detailed perspective.

CHAPTER FOUR*

The Relative Importance of Body Size, Phylogeny, Locomotion and Diet in the Evolution of Forelimb Dexterity in Carnivorans.

ABSTRACT

I examined the effects of body size, phylogenetic relatedness, diet (degree of vertebrate predation) and locomotion (arboreality) on the differential evolution of forelimb dexterity. Regression analyses indicate that although body size does appear to be positively correlated with the dexterity of the proximal components, once phylogenetic effects were accounted for, the relationship became non-significant. Phylogenetic relatedness was found to account for a significant amount of interspecific variation in proximal, distal and total (proximal + distal) dexterity. Similarly to body size, once phylogenetic effects were accounted for, arboreality was not significantly correlated with any of the dexterity scores. Vertebrate predation was significantly correlated with all three dexterity scores, albeit a negative. The amount of variation in the dexterity of proximal and distal components did, however, differ in magnitude within each significant result. Thus, each component can be differentially affected by specific functional demands. By examining the significant associations with diet and phylogeny and mapping the dexterity scores onto the phylogeny, I also demonstrate that the likely ancestral forelimb dexterity of both the caniform and feliform lineages was about average. Thus, forelimb dexterity has decreased or increased within particular lineages with reductions or elaborations in some species resulting from the invasion of specific niches not occupied by closely related species.

* This chapter is modified from a paper to be published in the Canadian Journal of Zoology.

INTRODUCTION

As discussed in previous chapters, forelimb dexterity should not be considered to be a property exclusive to the forepaws and the forelimb cannot be considered independently of the body. Thus, forelimb dexterity should be considered to be the result of the movements of distinct components which act in concert as a functional unit (see Chapter 2). In other words, the forelimb can be separated, both anatomically and behaviourally, into components which combine to produce skilled forelimb movements as in the dexterity index provided in Chapter 2. A similar approach has been adopted to investigate the evolution of avian flight (Gatesy and Dial 1996). In their study, Gatesy and Dial (1996) considered the hindlimbs, tail and wings of birds to be 'modules' which can be elaborated upon individually, or in combination with one another, to produce phenotypes with an array of flying skills. Using their approach as a model, I considered the proximal (shoulder, upper and lower forelimb) and distal (forepaw) parts of the forelimb as components (i.e. 'modules') which can be elaborated upon individually, or together, to produce a variety of manipulative skills. The dexterity index introduced in Chapter 2, allows for the separate examination of both the proximal and distal modules.

Given that the proximal and distal components are organised differently and can, potentially, be elaborated upon separately from one another, one would expect that the functional demands of different morphologies, phylogenetic histories and behaviours may be differentially related to the elaboration of each component. For example, overall body size is well known to play a significant role in the evolution of behavioural and ecological diversity (Damuth and MacFadden 1990; LaBarbera 1989; Schmidt-Nielsen 1984). Since the shape and function of individual elements of the forelimb can be affected by changes in body size (Biewener 1989), one might expect that body size may constrain or promote each component differently.

Similarly, if a species' ancestors possessed relatively poor proximal forelimb dexterity, it may be unlikely for extant species have a high degree of proximal dexterity. They may, however, be capable of elaborating upon their distal dexterity, resulting in an overall increase in manipulative prowess. Thus, phylogenetic relatedness may determine not only the degree of forelimb dexterity of a species, but also where the elaborations/reductions are likely to occur.

The most frequently cited reasons for interspecific differences in forelimb dexterity are, however, the behavioural demands of different lifestyles (Cartmill 1985; Gittleman 1986a; Whishaw et al. 1998). Both locomotion and diet have been previously cited as causally related to forelimb dexterity because of the functional demands placed upon the forelimbs during both activities. For example, arboreal locomotion has long been associated with high degrees of forelimb dexterity (Cartmill 1985). It has been assumed that movement through the trees requires grasping forepaws and this grasping ability is then transferred into non-locomotory activities. Grasping only involves the forepaws, whereas arboreal locomotion requires the active involvement of the entire forelimb. Therefore, arboreal locomotion may not necessarily be correlated with the dexterity of both forelimb components.

A corresponding argument has also been proposed for a correlation between vertebrate predation and forelimb dexterity (Gittleman 1986a; Hopson 1977). The capture of rapidly moving prey is thought to require extensive manipulation and rapid use of the forelimbs (Gittleman 1986a; Hopson 1977). Predation and manipulation may, however, require differential use of the proximal parts of the forelimbs and the forepaws. Thus, vertebrate predation may also affect the dexterity of the distal components separately from that of the proximal components.

Lastly, it may be instructive to determine the likely forelimb dexterity of ancestral species. The evolution from this ancestral state may be determined by the functional demands outlined above, but could also provide insight into the selective forces responsible for the observed variation in forelimb dexterity. The pattern of changes in forelimb dexterity across lineages may also suggest alternative explanations for observed behavioural diversity.

Therefore, I predicted that the following relationships would be present within carnivorans: 1) body size is negatively correlated with forelimb dexterity; 2) phylogeny plays a significant role in the variability of forelimb dexterity; 3) arboreality is positively correlated with forelimb dexterity; and 4) vertebrate predation is positively correlated with forelimb dexterity. These four predictions were then tested through regression analysis and modern comparative techniques.

METHODS

Behavioural Coding

To test the hypotheses that arboreality and vertebrate predation are both positively correlated with forelimb dexterity, the forelimb dexterity scores (Appendix 1) were compared against two other behavioural coding systems. Previous studies of locomotion and diet in carnivorans used either unordered categories (Gittleman 1986a, b; Van Valkenburgh 1985, 1987) or exact percentages (Gittleman and Harvey 1982). Behaviours rarely occur, however, as mutually exclusive categories and the use of precise proportions or percentages can be subject to change depending upon seasonal, geographical and methodological differences. I therefore chose to use indices which were based upon specific proportions/percentages in the literature, but were slotted into ordered categories which were gross enough such that seasonal and other minor fluctuations would not significantly affect species' coding. Thus, arboreality was coded as follows: '0', never climb trees; '1' capable of climbing, but do so rarely (i.e. scansorial); '2', good climbing skills and climb frequently (i.e. semi-arboreal); and '3', excellent climbing skills, capable of head-first, controlled descent (i.e. arboreal) (Appendix 1). Similarly, vertebrate predation was divided into four ordered categories contingent upon the estimated biomass of vertebrates in the diet: '0', < 25%; '1', 25-50%; '2', 50-75%; and '3' > 75% (Appendix 1). Where specific diet data were not available, an estimate of the dietary index, based upon available information, was used. Although this may reduce the reliability of this index, it was only necessary for four out of the 45 species.

Statistical Analysis

To assess the relationships between body size, phylogeny, arboreality and vertebrate predation and forelimb dexterity, it was necessary to perform three levels of analysis. Firstly, body size effects were controlled. The dexterity scores and body weights (from Nowak (1991)) were log-transformed and regressed against each other using least-squares linear regression (LaBarbera 1989). If a significant result was found, the residuals from that analysis were used in the subsequent analyses of phylogeny and behaviour.

The second method, autocorrelation, was used to assess the amount of interspecific variation which can be attributed to phylogeny. This method uses autoregression techniques to partition the total amount of variation in a trait into a phylogenetic and an environmental (i.e. adaptive) component (Cheverud et al. 1985; Harvey and Pagel 1991). A Moran's *I* statistic was used to determine the level at which autocorrelation should be performed (Gittleman and Kot 1990; Gittleman and Luh 1991). Through the use of a matrix which encodes the phylogenetic relatedness between the species of interest, predicted values of the trait can be calculated and correlated with the observed values to yield the amount of variation due to phylogeny.

To perform this analysis, the phylogenetic autocorrelation (PA) program was used (Luh et al. 1995). Although it has been shown that taxonomic ranks can be used just as effectively as branch lengths in autocorrelation (Gittleman and Luh 1991), the use of branch lengths is likely to produce more accurate and meaningful results simply due to the finer definition of interspecies relatedness provided by known branch lengths (Gittleman, pers. comm.; Gittleman and Luh 1991). Branch lengths were obtained from the Tables provided in Bininda-Edmonds et al. (1999).

Given that phylogenetic autocorrelation has been shown to be less reliable than other comparative methods (Garland, pers. comm.; Martins 1996; Martins and Garland 1991), I also employed nested ANOVAs of taxonomic levels to assess the relative importance of phylogeny in determining forelimb dexterity (Harvey and Pagel 1991). Although this method is dependent upon a detailed taxonomy of the species being studied, it is less controversial in its application than phylogenetic autocorrelation. The taxonomy provided by Wozencraft (1989) was used with amendments, where necessary, according to the Bininda-Edmonds et al. (1999) phylogeny.

Lastly, to examine the relationship between arboreality and vertebrate predation and forelimb dexterity, I performed ANOVAs of the three dexterity scores relative to the arboreality and diet scores. Since the use of species as independent data points violates the assumptions of independence in conventional statistics (Harvey and Pagel 1991; Chapters 2 and 3), I also employed Felsenstein's (1985) method of independent contrasts. As discussed in previous chapters, simulations of different comparative techniques have shown that independent contrasts is the most robust method (Diaz-Uriarte and Garland 1998, 1996; Garland et al. 1999) and yields the lowest type I error rates (Martins and Garland 1991). Since branch lengths were known, a gradual model of evolutionary change was used as it has been shown to be the most robust form of independent contrast analysis (Martins and Garland 1991).

This method requires a known phylogeny, which was taken from Bininda-Edmonds et al. (1999) (Appendix 3). The treatment of the domestic dog ,the maned wolf and was identical to that described in Chapter 2. Thus, the dog replaced the wolf on Bininda-Edmonds et al.'s (1999) phylogeny and the maned wolf and bush dog were resolved according to Wayne et al. (1997).

The phylogeny, branch lengths and dependent and independent variables were entered into the Comparative Analysis of Independent Contrasts (CAIC) program (Purvis and Rambaut 1995). All of the traits were considered to be continuous. Proper standardisation of the data was tested by regressing the absolute value of the contrasts against the the square-root of the branch lengths (Garland et al. 1993). None of the regressions were significant (Table 4.1), indicating that the data was properly standardised. Normality of the data was then tested with a Shapiro-Wilk W test for each variable (JMPIN v 3.2 SAS Institute). All of the dependent variables (i.e. dexterity scores) were normally distributed, but the independent variables were not ($W_{\text{arboreality}} = 0.86, P < 0.01$; $W_{\text{diet}} = 0.75, P < 0.01$). Log, square-root and cube-root transformations were not successful in normalising the data, so the untransformed contrasts were used in subsequent regression analyses. Although the lack of a normal distribution in the independent variable can be problematic in regressions, the normal distribution of the

Table 4.1. Results from the regression analysis of the absolute value of the contrasts against the square root of the branch lengths of the phylogeny (all d.f. = 1, 42).

Contrast	*F*	*P*
Proximal Dexterity	3.51	0.07
Distal Dexterity	0.28	0.60
Total Dexterity	0.31	0.58
Arboreality	3.58	0.07
Vertebrate Predation	1.16	0.29

dependent variable is a more crucial assumption (Daniel 1991). Therefore, despite the possibility of non-parametrics being affected by the repeated zeros present in independent contrasts (Garland et al. 1993), Spearman-rank correlations were also performed.

The dexterity contrasts were regressed against the arboreality and vertebrate predation contrasts through the origin (Garland et al. 1992) using reduced major axis regression formulae. An *F*-test was used to assess significance. Although it could be argued that a multivariate approach may be more appropriate, the purpose of this study is to assess the effect of different independent variables upon each forelimb component.

Lastly, to ascertain the pattern of evolutionary change in forelimb dexterity, I mapped the three dexterity scores onto Bininda-Edmonds et al.'s (1999) phylogeny using MacClade v. 3.05 (Maddison and Maddison 1992). Although the dexterity index is not continuous in the true sense (i.e. cannot have a total dexterity of 6.71), the presence of large integers (i.e. above 10) precluded the use of the discrete character algorithms and therefore, all of the dexterity scores were treated as continuous variables. Two algorithms were chosen to determine the ancestral states of the 'basal' carnivoran (i.e. base of entire tree) and that of the basal caniform and feliform nodes. The first of these methods was a linear parsimony model which is based upon minimising the sum of the evolutionary changes occurring across the entire tree (Martins and Hansen 1996). Although this is the most commonly used method of ancestral state reconstruction (Martins and Lamont 1998), it can be problematic when the rate of evolution is not slow (Martins and Hansen 1996) and often yields multiple solutions (Swofford and Maddison 1987). A second, more robust method was therefore implemented as well. The sum-of-squared changes parsimony model minimises the sum of the squared changes across the entire tree

(Martins and Hansen 1996). This model is not only representative of different rates of evolutionary change (e.g. Brownian motion), it also yields a single value for each node.

RESULTS

Body Size

All three dexterity indices were positively correlated with body size, but only the correlation between proximal dexterity index and body size was significant ($F = 9.49$, df = 1, 43, $P < 0.05$). This suggests that with increasing body size, there is a significant increase in proximal forelimb dexterity. Given that this analysis does not incorporate phylogeny, and could be affected by non-independence of data, the independent contrasts approach was also applied to the analysis of body size. Once the effects of phylogeny were accounted for, the relationship between proximal dexterity and body size became non-significant ($F = 0.0004$, df = 1, 42, $P = 0.99$). Distal and total dexterity scores and body size relationships remained non-significant.

Phylogeny

The results of the Moran's I test indicated that phylogenetic distance is significantly correlated with all three dexterity scores (Figure 4.1). Subsequent autocorrelation determined that the amount of interspecific variation explained by phylogenetic relatedness varied between the dexterity scores (Table 4.2).

Similar results occurred with the nested ANOVAs of taxonomic ranks (Table 4.3). The only significant difference between ranks was at the level of suborder. That is, between ≈ 10 and 20 % of the variation in dexterity scores was attributable to whether a given species was a caniform or feliform.

Figure 4.1: The results of the Moran's *I* test on the three dexterity scores. The x-axis represents the divergence time of the nodes of the phylogeny in millions of years ago (mya) and is based on branch length estimates provided in Bininda-Edmonds et al. (1999). The y-axis represents the *Z* scores calculated by the PA (Phylogenetic Autocorrelation) program (Luh et al. 1995) for the nodes. Since all three dexterity scores possess *Z* scores greater than 1.96 at one or more phylogenetic distances, they exhibit phylogenetic autocorrelation (Gittleman, pers. comm.; Luh et al. 1995).

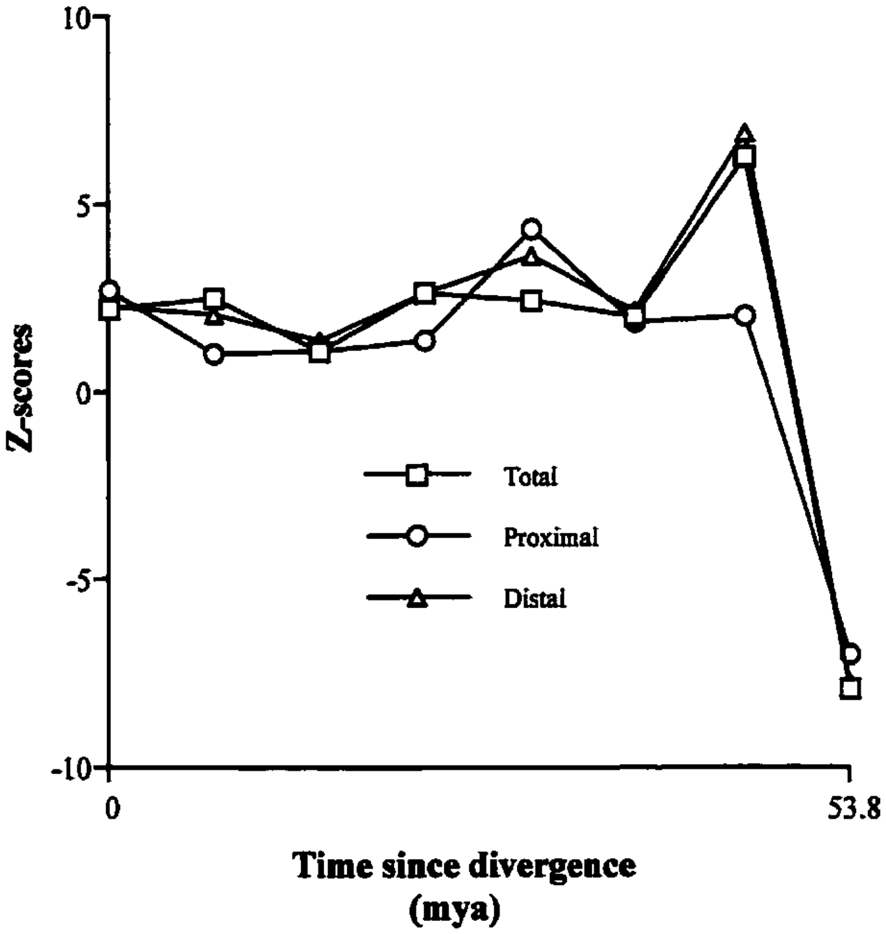

10
5
0
-5
-10
Z-scores
0
53.8
Time since divergence
(mya)
Total
Proximal
Distal

Table 4.2. Autocorrelation results for the three dexterity indices in which 'alpha' is the statistical power of the weighting matrix, 'rho' is the autocorrelation coefficient and 'r^2' refers to the amount of the total variation accounted for by phylogeny (i.e Pearson r).

	Alpha	Rho	r^2
Proximal dexterity	9.30	0.37	0.27
Distal dexterity	7.90	0.27	0.14
Total dexterity	7.35	0.27	0.15

Table 4.3. Results of nested ANOVAs of the three dexterity scores.

Dexterity score	Taxonomic level	*F*	d.f.	*P*	r^{2a}
Proximal	Suborder	4.93	1, 43	0.03	0.10
	Family	1.97	7, 37	0.27	—
	Genus	0.70	27, 17	0.80	—
Distal	Suborder	10.30	1, 43	< 0.01	0.19
	Family	1.86	7, 37	0.10	—
	Genus	0.56	27, 17	0.92	—
Total	Suborder	8.49	1, 43	0.01	0.16
	Family	1.92	7, 37	0.09	—
	Genus	0.58	27, 17	0.90	—

[a] note that only the r^2's of significant taxonomic levels are shown.

Arboreality

ANOVAs of the species as independent data points indicated that there were significant differences in all three dexterity scores with respect to arboreality (Table 4.4). Subsequent Tukey-Kramer tests indicated that species which scored a '0' or '1' had significantly lower dexterity scores than those that scored a '2'. Thus, nonarboreal and scansorial species had

significantly lower dexterity scores than semiarboreal species, but fully arboreal species were not significantly different from the other three categories.

These results were not, however, corroborated by regression analyses of the independent contrasts. Only the regression of the proximal dexterity contrasts against arboreality yielded a significant relationship (Table 4.5). The presence of an outlier, the contrast between the brown bear (*Ursus arctos*) and the polar bear (*Ursus maritimus*), appeared to alter both the correlation coefficient (r^2) and the slope of the regression line and was well outside of the statistically acceptable range of two standard deviations (contrast value = average of 4.2 standard deviations from the regression lines) (Figures 4.2a, 4.3a, 4.4a). For this reason, the r^2's and slopes are shown for those regression lines including and excluding this contrast (Table 4.5). Removal of this rogue point resulted in no significant correlations (Table 4.5). Thus, with an increase in arboreality, there is no correlated change in proximal, distal or total dexterity. This was corroborated by the results of Spearman rank correlations of the contrasts ($Z_{\text{proximal}} = 1.65$, n = 44, $P > 0.05$; $Z_{\text{distal}} = 1.55$, n = 44, $P > 0.10$; $Z_{\text{total}} = 1.64$, n = 44, $P > 0.10$).

Vertebrate Predation

ANOVAs of the species as independent data points indicated that there were no significant differences in proximal dexterity across the diet scores, but there were significant differences for both distal and total dexterity (Table 4.4). Subsequent Tukey-Kramer tests indicated that species which scored a '0' had significantly higher dexterity scores than those that scored a '3'. That is, species which relied less heavily upon vertebrates as part of their diet had higher degrees of distal and total dexterity than those which were primarily vertebrate predators.

These findings were corroborated by regression analyses of the independent contrasts as all three dexterity scores exhibited significant, negative correlations with the percentage of vertebrates in the diet (Table 4.5). As with the arboreality regressions, the brown bear-polar bear contrast was a rogue point (Figure 4.2b, 4.3b, 4.4b). Despite the changes in slope and r^2 when the rogue point was excluded, the significance of the results was the same: all three dexterity scores were significantly correlated with vertebrate predation (Table 4.5). Contrary to the prediction, however, dexterity was found to decrease with increasing degrees of vertebrate predation. Thus, species which rely more upon vertebrates have lower degrees of dexterity in both proximal and distal components. This was only partially supported by Spearman rank correlations of the contrasts ($Z_{proximal} = -1.73$, $n = 44$, $P > 0.05$; $Z_{distal} = -2.31$, $n = 44$, $P < 0.05$; $Z_{total} = -1.94$, $n = 44$, $P < 0.05$).

Character Mapping

Linear parsimony reconstruction of the proximal, distal and total dexterity scores indicated fairly low scores with multiple solutions for the basal caniform, feliform and carnivoran nodes (Table 4.6). Sum-of-squared-changes parsimony yielded higher, but more precise, dexterity scores for each of the nodes (Table 4.6, Figures 4.6, 4.7, 4.8).

Table 4.4. The results of the ANOVAs of the dexterity scores relative to the arboreality and diet scores (all d.f. = 3, 41).

	Dexterity score	*F*	*P*
Arboreality	Proximal	7.70	< 0.01
	Distal	5.55	< 0.01
	Total	6.74	< 0.01
Diet	Proximal	2.04	0.12
	Distal	3.44	0.03
	Total	2.95	0.04

Figure 4.2: Scatter plots of the independent contrasts of the proximal dexterity scores against: **a)** arboreality and **b)** diet. The rogue contrast between the brown bear (*Ursus arctos*) and the polar bear (*Ursus maritimus*) is indicated by the '**U**'. The dotted line refers to the reduced major axis regression line including the rogue point and the solid line refers to the regression line excluding the rogue point. Similar relationships also occurred for the other two dexterity scores (see Table 4.5, Figures 4.3, 4.4).

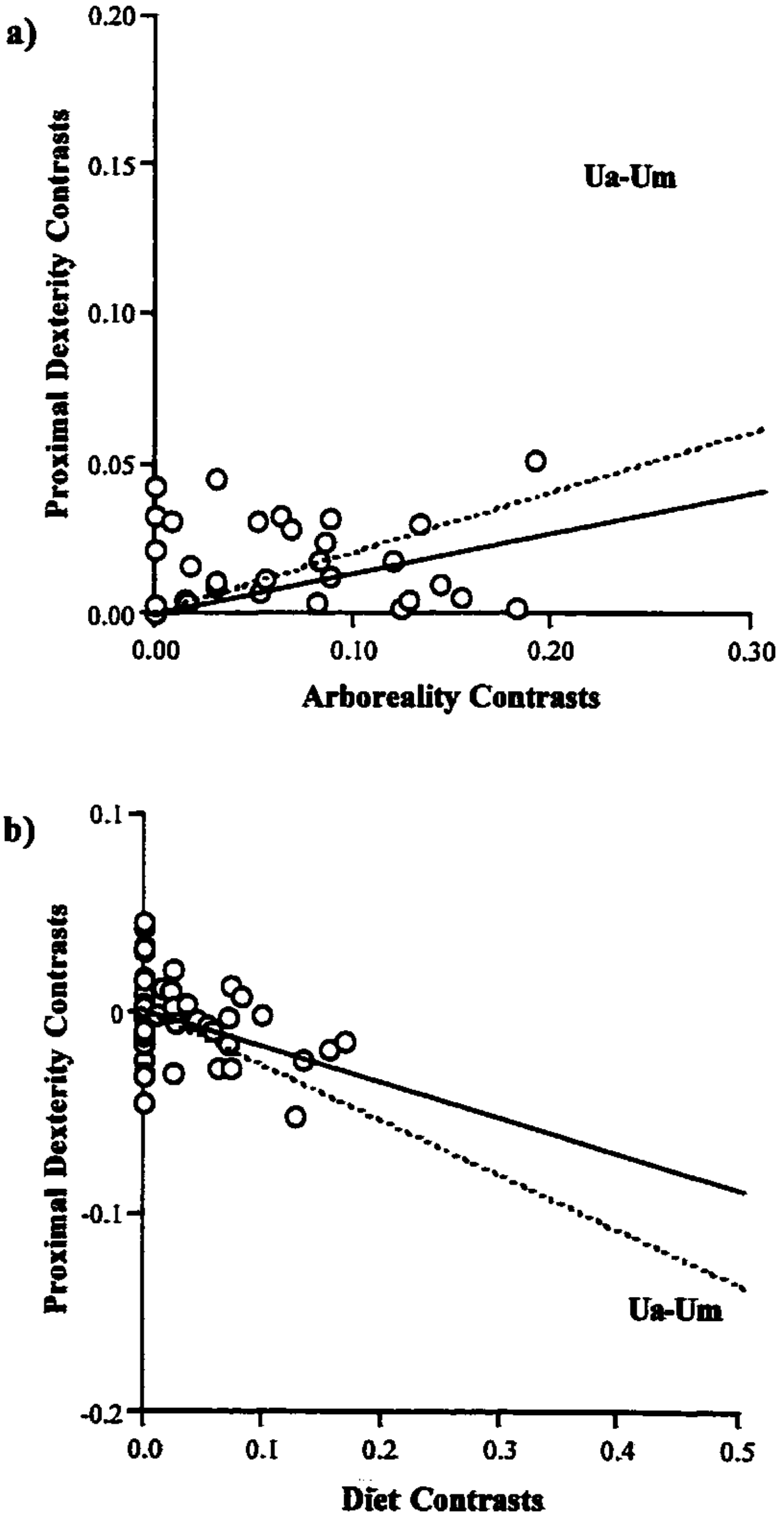
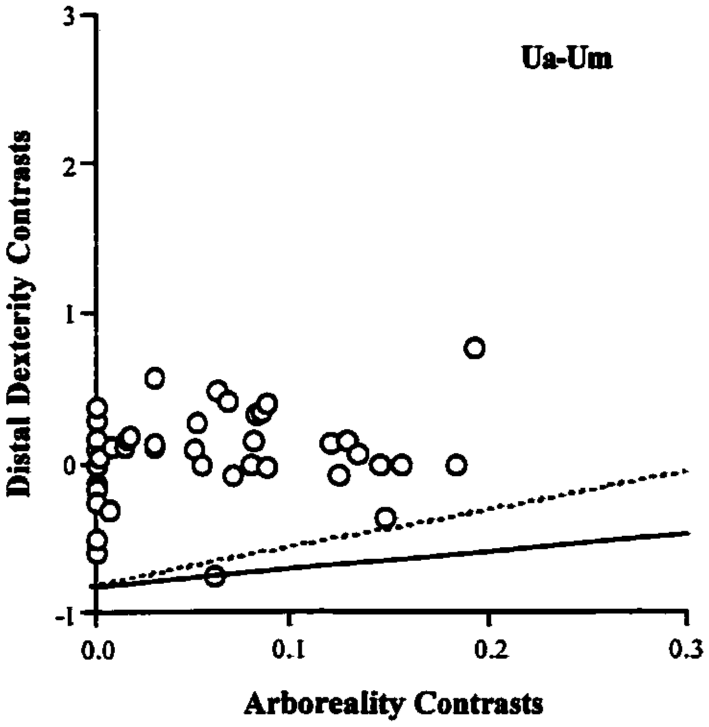

a)
0.20
0.15
0.10
0.05
0.00
Proximal Dexterity Contrasts
Ua-Um
0.00
0.10
0.20
0.30
Arboreality Contrasts
b)
0.1
0
-0.1
-0.2
Proximal Dexterity Contrasts
Ua-Um
0.0
0.1
0.2
0.3
0.4
0.5
Diet Contrasts

Figure 4.3: Scatter plots of the independent contrasts of the distal dexterity scores against: **a)** arboreality and **b)** diet. The rogue contrast between the brown bear (*Ursus arctos*) and the polar bear (*Ursus maritimus*) is indicated by the '**U**'. The dotted line refers to the reduced major axis regression line including the rogue point and the solid line refers to the regression line excluding the rogue point. Similar relationships also occurred for the other two dexterity scores (see Table 4.5, Figures 4.2, 4.4).

a)


Ua-Um
Distal Dexterity Contrasts
3
2
1
0
-1
0.0
0.1
0.2
0.3
Arboreality Contrasts

b)

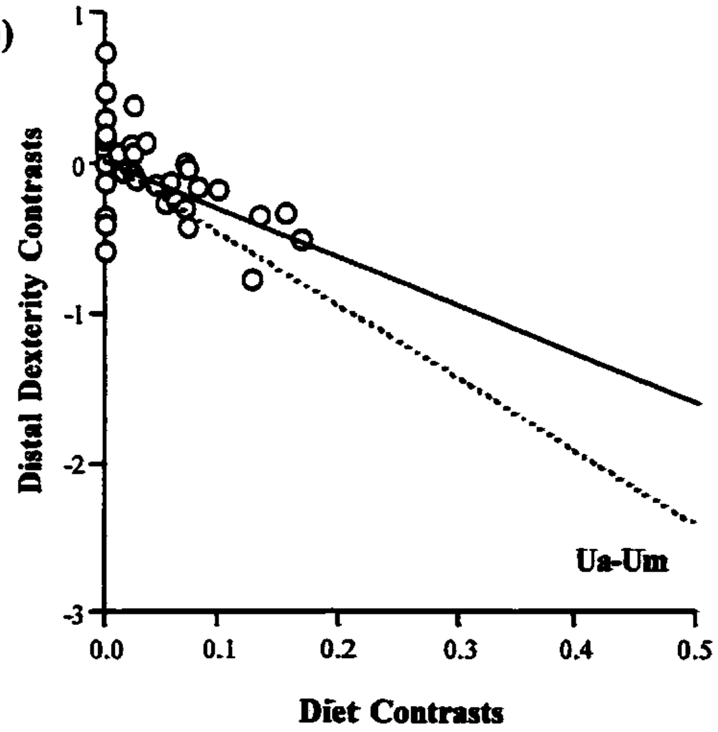

Ua-Um
Distal Dexterity Contrasts
1
0
-1
-2
-3
0.0
0.1
0.2
0.3
0.4
0.5
Diet Contrasts

Figure 4.4: Scatter plots of the independent contrasts of the total dexterity scores against: **a)** arboreality and **b)** diet. The rogue contrast between the brown bear (*Ursus arctos*) and the polar bear (*Ursus maritimus*) is indicated by the '**U**'. The dotted line refers to the reduced major axis regression line including the rogue point and the solid line refers to the regression line excluding the rogue point. Similar relationships also occurred for the other two dexterity scores (see Table 4.5, Figures 4.2, 4.3).

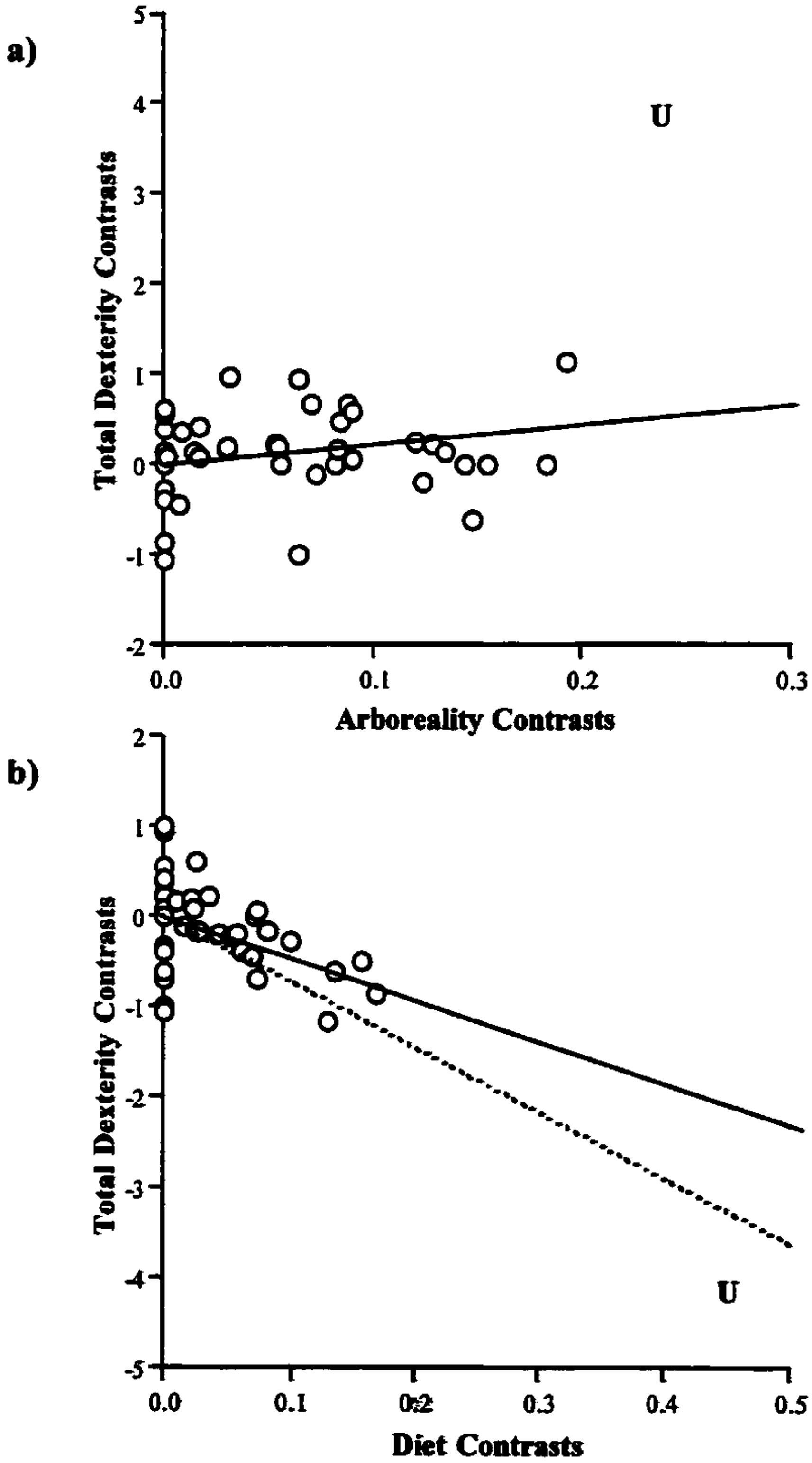

a)
U
Total Dexterity Contrasts
5
4
3
2
1
0
-1
-2
0.0
0.1
0.2
0.3
Arboreality Contrasts
b)
U
Total Dexterity Contrasts
2
1
0
-1
-2
-3
-4
-5
0.0
0.1
0.2
0.3
0.4
0.5
Diet Contrasts

Table 4.5. The slopes (β) and r^2 values for the regression lines of the three dexterity indices against arboreality and vertebrate predation (Diet). 'With' and 'without' refers to the inculsion or exclusion of the rogue brown bear-polar bear contrast.

		With		Without	
		β	r^2	β	r^2
Arboreality	Proximal	6.78	0.24*	9.58	0.10
	Distal	0.84	0.17	0.39	0.10
	Total	1.33	0.18	0.66	0.11
Diet	Proximal	-4.46	0.52**	-2.92	0.48**
	Distal	-4.05	0.70**	-2.64	0.28**
	Total	-6.07	0.66**	-3.96	0.23*

* $P < 0.05$

** $P < 0.01$

Figure 4.5: The reconstruction of the ancestral states of the proximal dexterity score using sum-of-squared changes parsimony to trace the pattern of evolutionary change over the Bininda-Edmonds et al. (1999) phylogeny. The three numbered nodes are as follows: 1 - basal carnivoran, 2 - basal caniform and 3 - basal feliform. The exact values for these three nodes, as well as those of the other two dexterity scores are provided in Table 4.6.

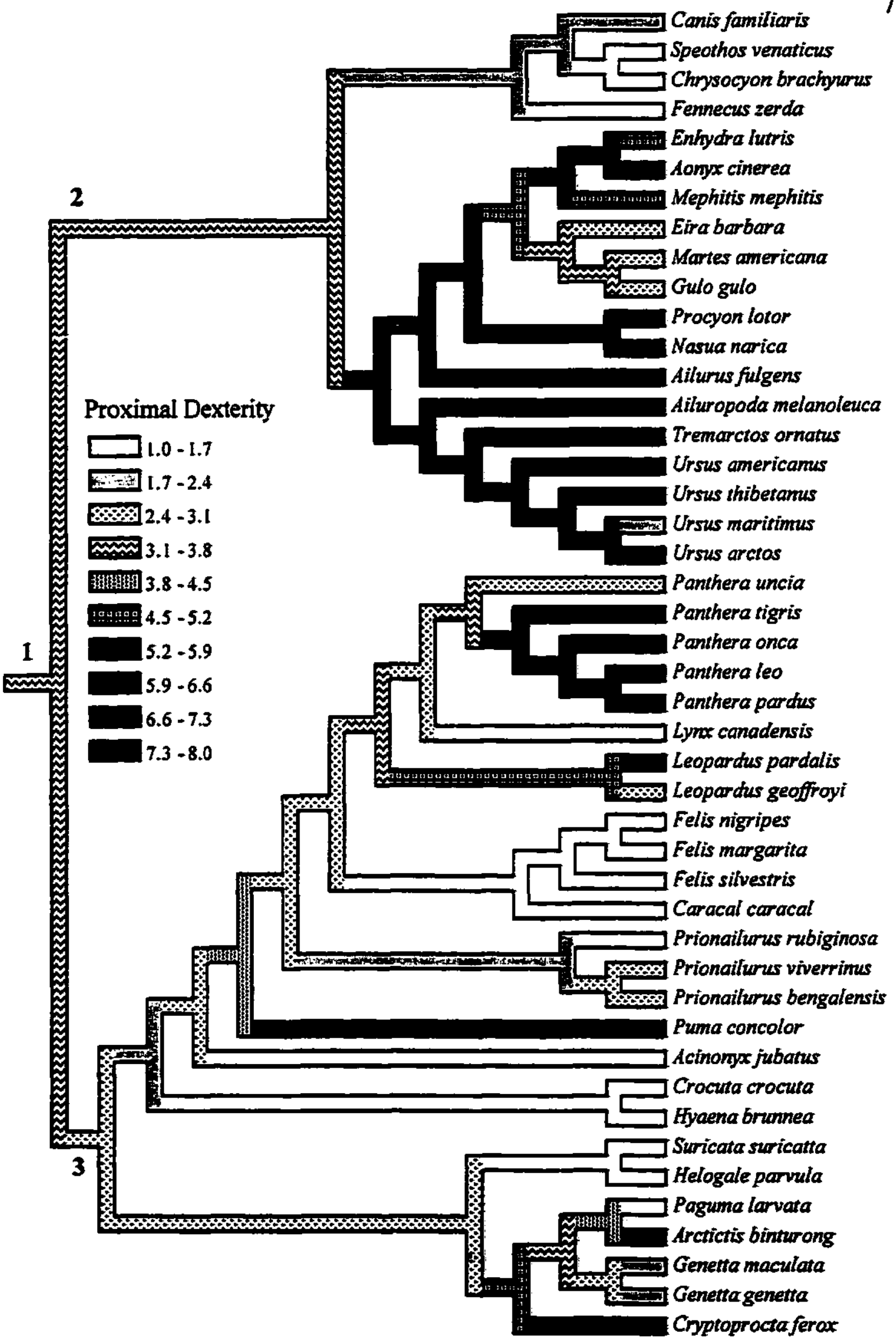

Canis familiaris
Speothos venaticus
Chrysocyon brachyurus
Fennecus zerda
Enhydra lutris
Aonyx cinerea
Mephitis mephitis
Eira barbara
Martes americana
Gulo gulo
Procyon lotor
Nasua narica
Ailurus fulgens
Ailuropoda melanoleuca
Tremarctos ornatus
Ursus americanus
Ursus thibetanus
Ursus maritimus
Ursus arctos
Panthera uncia
Panthera tigris
Panthera onca
Panthera leo
Panthera pardus
Lynx canadensis
Leopardus pardalis
Leopardus geoffroyi
Felis nigripes
Felis margarita
Felis silvestris
Caracal caracal
Prionailurus rubiginosa
Prionailurus viverrinus
Prionailurus bengalensis
Puma concolor
Acinonyx jubatus
Crocuta crocuta
Hyaena brunnea
Suricata suricatta
Helogale parvula
Paguma larvata
Arctictis binturong
Genetta maculata
Genetta genetta
Cryptoprocta ferox
1
2
3
Proximal Dexterity
1.0 - 1.7
1.7 - 2.4
2.4 - 3.1
3.1 - 3.8
3.8 - 4.5
4.5 - 5.2
5.2 - 5.9
5.9 - 6.6
6.6 - 7.3
7.3 - 8.0

Figure 4.6: The reconstruction of the ancestral states of the distal dexterity score using sum-of-squared changes parsimony to trace the pattern of evolutionary change over the Bininda-Edmonds et al. (1999) phylogeny. The three numbered nodes are as follows: 1 - basal carnivoran, 2 - basal caniform and 3 - basal feliform. The exact values for these three nodes, as well as those of the other two dexterity scores are provided in Table 4.6.

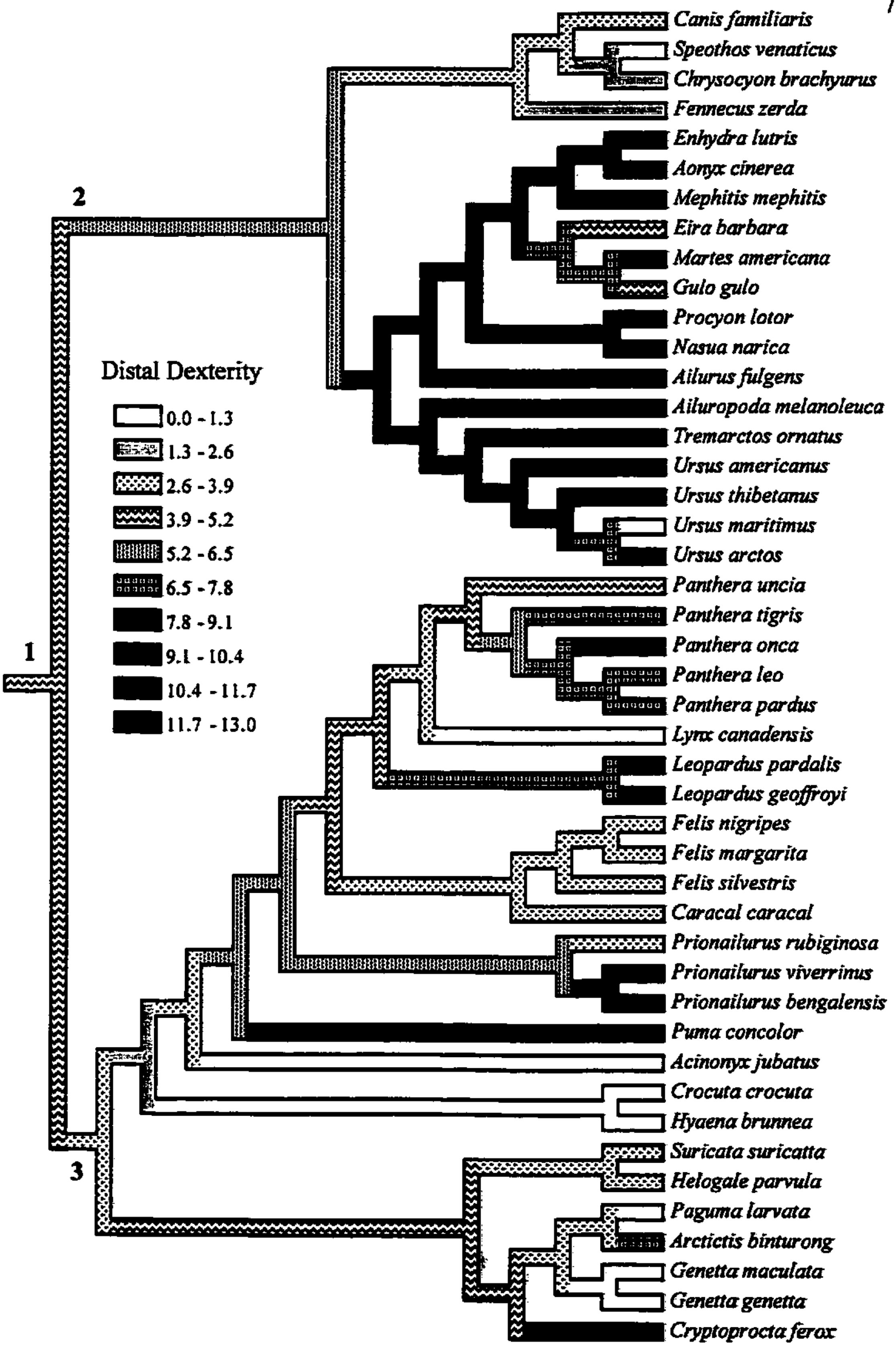

Canis familiaris
Speothos venaticus
Chrysocyon brachyurus
Fennecus zerda
Enhydra lutris
Aonyx cinerea
Mephitis mephitis
Eira barbara
Martes americana
Gulo gulo
Procyon lotor
Nasua narica
Ailurus fulgens
Ailuropoda melanoleuca
Tremarctos ornatus
Ursus americanus
Ursus thibetanus
Ursus maritimus
Ursus arctos
Panthera uncia
Panthera tigris
Panthera onca
Panthera leo
Panthera pardus
Lynx canadensis
Leopardus pardalis
Leopardus geoffroyi
Felis nigripes
Felis margarita
Felis silvestris
Caracal caracal
Prionailurus rubiginosa
Prionailurus viverrinus
Prionailurus bengalensis
Puma concolor
Acinonyx jubatus
Crocuta crocuta
Hyaena brunnea
Suricata suricatta
Helogale parvula
Paguma larvata
Arctictis binturong
Genetta maculata
Genetta genetta
Cryptoprocta ferox
1
2
3
Distal Dexterity
0.0 - 1.3
1.3 - 2.6
2.6 - 3.9
3.9 - 5.2
5.2 - 6.5
6.5 - 7.8
7.8 - 9.1
9.1 - 10.4
10.4 - 11.7
11.7 - 13.0

Figure 4.7: The reconstruction of the ancestral states of the total dexterity score using sum-of-squared changes parsimony to trace the pattern of evolutionary change over the Bininda-Edmonds et al. (1999) phylogeny. The three numbered nodes are as follows: 1 - basal carnivoran, 2 - basal caniform and 3 - basal feliform. The exact values for these three nodes, as well as those of the other two dexterity scores are provided in Table 4.6.

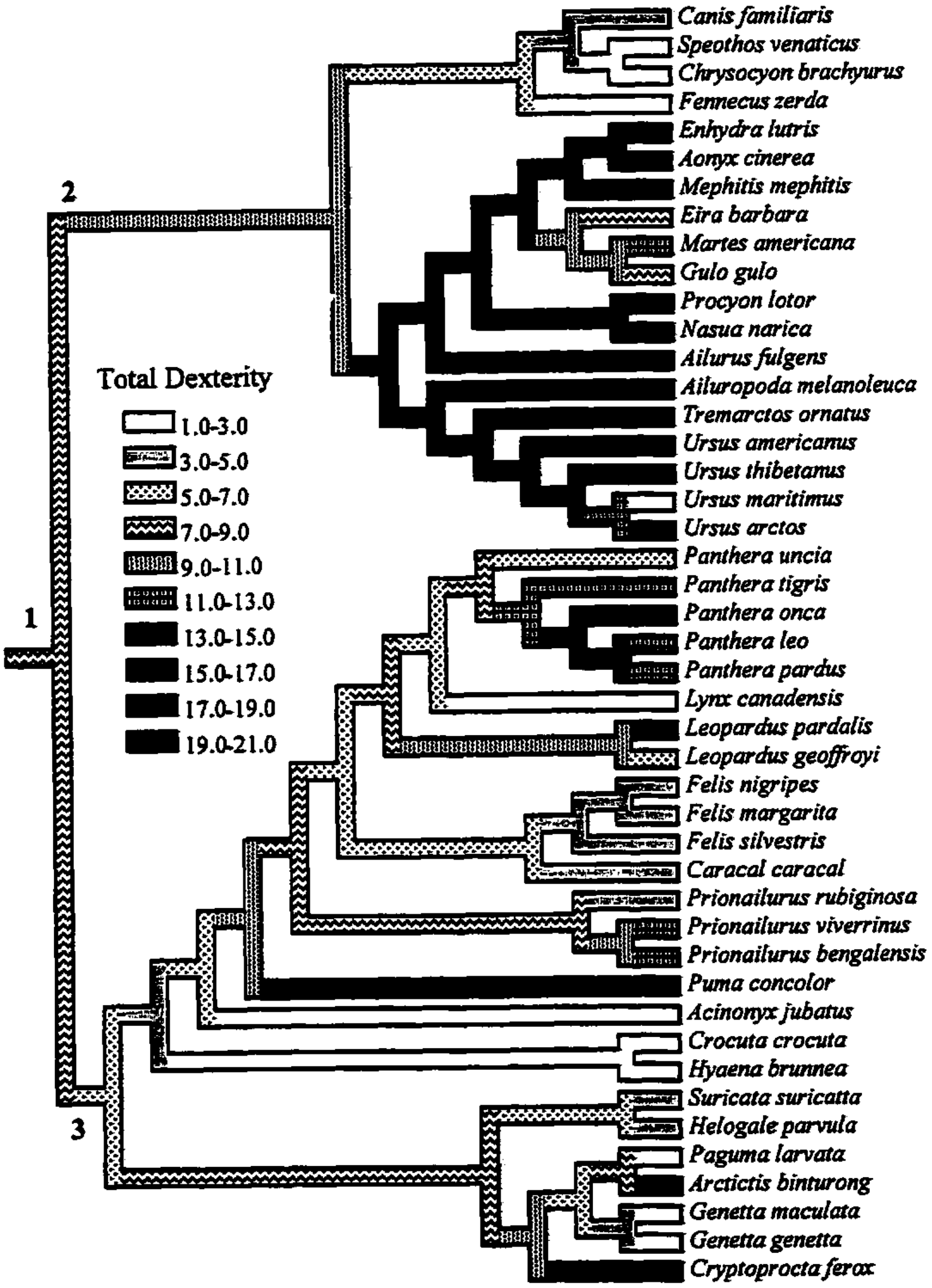

2
1
3
Total Dexterity
1.0-3.0
3.0-5.0
5.0-7.0
7.0-9.0
9.0-11.0
11.0-13.0
13.0-15.0
15.0-17.0
17.0-19.0
19.0-21.0
Canis familiaris
Speothos venaticus
Chrysocyon brachyurus
Fennecus zerda
Enhydra lutris
Aonyx cinerea
Mephitis mephitis
Eira barbara
Martes americana
Gulo gulo
Procyon lotor
Nasua narica
Ailurus fulgens
Ailuropoda melanoleuca
Tremarctos ornatus
Ursus americanus
Ursus thibetanus
Ursus maritimus
Ursus arctos
Panthera uncia
Panthera tigris
Panthera onca
Panthera leo
Panthera pardus
Lynx canadensis
Leopardus pardalis
Leopardus geoffroyi
Felis nigripes
Felis margarita
Felis silvestris
Caracal caracal
Prionailurus rubiginosa
Prionailurus viverrinus
Prionailurus bengalensis
Puma concolor
Acinonyx jubatus
Crocuta crocuta
Hyaena brunnea
Suricata suricatta
Helogale parvula
Paguma larvata
Arctictis binturong
Genetta maculata
Genetta genetta
Cryptoprocta ferox

Table 4.6. The ancestral states of the three dexterity scores, using two models of reconstruction, at the three basal nodes of the carnivore phylogeny (see Appendix 1).

Model	Dexterity score	Basal carnivore	Basal caniform	Basal feliform
Linear parsimony	Proximal	3-4	3-4	3-4
	Distal	2-3	2-3	2-3
	Total	3-4	3-4	3-4
Sum-of-squared changes parsimony	Proximal	3.3	3.7	2.9
	Distal	4.9	5.9	3.8
	Total	8.2	9.6	6.7

DISCUSSION

Both phylogeny and vertebrate predation explained a significant amount of the interspecific variation in forelimb dexterity in carnivorans, the strongest relationship (i.e. highest r^2) being that between proximal forelimb dexterity and vertebrate predation (Table 4.5). The amount of variation did, however, vary within the independent variables examined, thus supporting my view that the components of the forelimb can be elaborated upon separately in response to different functional demands.

Body Size

Overall body size plays a significant part in most aspects of an organism's biology (Damuth and MacFadden 1990; LaBarbera 1989; Schmidt-Nielsen 1984). Despite this fact, none of the dexterity scores were found to be significantly correlated with body size. This would appear to be related to a strong phylogenetic component in the variation of both forelimb dexterity (see below) and body size (Gittleman 1986b).

A second characteristic of body size which may have obscured any relationship with forelimb dexterity is that body size is the result of a large number of selective forces which act independently of forelimb dexterity (Damuth and MacFadden 1990; LaBarbera 1989; Schmidt-Nielsen 1984). Therefore, in most species, the interactions between body size and many different factors are likely to be relatively stronger than any possible relationship between body size and dexterity. Thus, large species, depending upon their phylogenetic history and diet (see below) are equally likely to have evolved high degrees of forelimb dexterity as smaller species.

Phylogeny

The phylogenetic, or inherited, portion of variation in a trait can have a significant effect on the evolution of behaviours (Harvey and Pagel 1991). Phylogenetic relatedness accounted for a significant amount of the interspecific variation in all three dexterity scores. This suggests that there are some phylogenetic constraints which may shape the evolution of forelimb dexterity in carnivorans. How and why this occurs is difficult to resolve. It may occur due to phylogenetic time lags, developmental constraints, phylogenetic niche conservatism or a myriad of other possibilities (Harvey and Pagel 1991).

Studies of forelimb dexterity in other mammalian taxa do support a significant phylogenetic effect on forelimb use. For example, Whishaw et al. (1998), from an examination of forelimb use and food handling in 10 different rodent species, concluded that not only do rodents appear to share a common structural pattern in their forelimb movements during feeding, but that species which are more closely related to one another tend to be more similar in their forelimb use than those that are distantly related. Similarly, in Bishop's (1964) study of forelimb use in primates, species which belonged to the same families had a tendency to exhibit more similar forelimb use patterns to one another than to species in other families. For example, lorises (family Loridae) possess a common set of forelimb movements which they use to capture prey, whereas bushbabies (family Galagidae) execute a different set of forelimb movements. Corroborating evidence is found more recently within species of marmosets and tamarins (Singer and Schwibbe 1999). Thus, there is a tendency for mammalian taxa to share a common set of forelimb movements, and dexterity, which is supported by the present results.

Arboreality

Arboreal locomotion, the movement of an animal through the trees, has been regarded as a key factor promoting complex forelimb use (Cartmill 1985; Nudo and Masterton 1990; Wood-Jones 1916). Although the analysis of the 'raw' data indicated that there is a relationship between climbing skill and forelimb dexterity (Table 4.4), the more robust independent contrasts results showed no such relationship (with the possible exception of proximal dexterity) (Table 4.5). This may be, in part, due to the lack of extreme of arboreal specialisations in the carnivorans examined, but it also suggests that grasping forepaws may not be an essential part of moving through the trees in carnivorans.

Arboreal locomotion can, in fact, be facilitated by a number of other morphological adaptations apart from grasping forepaws. For example, claws may be used to secure purchase on tree trunks. Within the species examined, the American pine marten (*Martes americana*) possesses a relatively mediocre degree of forelimb dexterity (Appendix 1), yet it is capable of rapidly pursuing squirrels through the trees (Clark et al. 1987). Rather than implementing grasping forepaws, the marten has needle-sharp claws which serve the dual purposes of retaining contact with the substrate during arboreal locomotion and facilitating effective prey capture. The use of claws in arboreal locomotion also occurs in members of other taxa such as the marsupial phascogales (*Phascogale* spp.) and North American tree squirrels (*Sciurus* spp. and *Tamiasciurus* spp.). Other mechanisms may also be used which do not rely upon grasping such as adhesion (reptiles and amphibians) and suction (some bats) (Cartmill 1985). Thus, arboreal locomotion does not necessarily require grasping forepaws and, consequently, need not be directly correlated with forelimb dexterity.

Vertebrate Predation

Predatory behaviour, specifically the capture of vertebrate prey, has been considered to be a promoting factor of forelimb dexterity (Gittleman 1986a; Hopson 1977). That is, species which capture vertebrates possess higher degrees of forelimb dexterity than those which do not. Contrary to this theory, my results demonstrate that although a significant correlation does exist between forelimb dexterity and vertebrate predation, it is negative rather than positive. Thus, species which feed almost exclusively upon vertebrates tend to have a lower degree of forelimb dexterity than species feeding on other items.

Although predatory species, in general, do require considerable skill in the use of their forelimbs to successfully capture and manipulate prey, they also require the ability to chase down prey. This ability is evident even in ambush predators which may have to pursue potential prey in short chases prior to capture. This locomotor requirement may have placed limitations on the flexibility of the forelimbs, despite their use as prey-capture organs. An examination of detailed descriptions of predatory behaviour (Ben-David et al. 1991; Eisenberg and Leyhausen 1972; Leyhausen 1979; Pellis and Officer 1987) indicates that although the manipulative movements are rapid, precise, skilled movements of the distal components are relatively unimportant. Rather, it is the proper placement of the teeth which is of utmost importance in subduing prey. In fact, in some species, complex patterns of prey capture can occur in species with relatively poor proximal and distal dexterity (e.g. opossums (*Monodelphis domestica*) in Ivanco et al. 1996). Thus a combination of locomotor requirements and a lack of intensive selection for high degrees of dexterity in predatory species may limit the degree of dexterity exhibited in both proximal and distal components.

In contrast to predatory species, omnivorous species do not require locomotor adaptations for pursuing prey since they are generally opportunistic. Also, by definition, omnivores feed upon a wide variety of foods which can range considerably in their shape, size and texture. To feed upon such a wide variety of foods and manipulate them effectively probably requires a greater degree of distal dexterity than prey capture (Ivanco et al. 1996; Iwaniuk et al. 1998). Furthermore, the ability to mechanically process foodstuffs could be improved by using the forelimb to manipulate and/or process items such that maximal processing efficiency can occur (Iwaniuk 1996). Thus, the comparative lack of locomotor restrictions and possible selection for higher degrees of forelimb dexterity is likely to result in higher degrees of forelimb dexterity in omnivores.

It should be noted, however, that some of the species given a low vertebrate predation score, such as the crustacean specialist, the small-clawed otter (*Aonyx cinerea*) and the herbivorous giant panda, are not true omnivores. These species are, in fact, dietary specialists in much the same way as vertebrate predators. The key difference in these two species is that their dietary specialisations require high degrees of forelimb dexterity. For example, in the small-clawed otter, crabs and other aquatic invertebrates are taken underwater from fissures and under rocks (Kruuk et al. 1994). This kind of extractive foraging is likely to promote forelimb dexterity, as it has in other extractive foragers (e.g. capuchin monkeys (*Cebus* spp.)), because finely tuned movements are an advantage in foraging for and grasping prey underneath and within different objects. The giant panda, however, feeds mainly upon bamboo (Schaller et al. 1989) which does not require extractive foraging techniques. By being able to manipulate bamboo culms, the giant panda may be able to mechanically process the bamboo more effectively and therefore consume more bamboo per sitting. Support for this theory is found in the similar manipulative behaviours which have been reported for gentle lemurs (*Hapalemur griseus*) feeding on bamboo (Stafford et al. 1993). Thus, in general, forelimb dexterity decreases with vertebrate predation, which is suggestive of a correlation between omnivory and dexterity, but specific dietary specialisations can also promote forelimb dexterity.

Ancestral States

The reconstruction of the dexterity scores at ancestral nodes indicates that the ancestor of each of two major lineages and that of the entire order had moderate to low dexterity. The examination of the pattern of evolutionary changes across lineages further indicates that, in some cases, particular changes in forelimb dexterity characterise entire lineages. For example, within the canids, forelimb dexterity has decreased, but it has increased within the ursids (Figures 4.6, 4.7, 4.8). In some lineages, however, there are species which are drastically different in their forelimb dexterity than their closest relatives. One such example is the polar bear. In comparison to the rest of the ursids, the polar bear is unique in that it has lost the majority of its forelimb dexterity. This can best be explained by the niche occupied by the polar bear. Unlike other ursids, the polar bear is almost entirely carnivorous and ranges over tundra regions. In order to move efficiently over large distances in search of prey (up to 300 km per season (Schweinsburg and Lee 1982; Stirling et al. 1978)), the polar bear also possesses a suite of morphological and behavioural adaptations which set it apart from its closest relatives such as longer, stiffer limbs, a longer trunk and dense mats of fur covering the paws (Renous et al. 1998). This strong reliance upon efficient locomotion appears to have been at the expense of forelimb dexterity as they possess significantly lower dexterity scores than other bears. Thus, in the polar bear, the requirements of locomotion seem to have superseded that of forelimb dexterity.

Similar arguments can be made for species differences within other clades, the point being that forelimb dexterity may also be an adaptive response to selection pressures specific to a species. As such, changes in forelimb dexterity may also be viewed as an integral part of invading specific niches. For example, there is a tendency for riparian species (those species inhabiting watercourses) to have relatively high degrees of forelimb dexterity than closely related species (e.g. raccoon, small-clawed otter, Indian fishing cat (*Prionailurus viverrinus*)). Although a causal mechanism cannot be inferred from correlational analyses, the relationship between riparian foraging and forelimb dexterity may be indicative of a functional response to an overall niche. To determine whether niche metrics can be related to forelimb dexterity will, however, require study of a broader range of species and more detailed information on the dietary habits of the species examined.

CONCLUSIONS

Body size and climbing ability are not related to the forelimb dexterity of carnivorans, but phylogeny and vertebrate predation are significantly correlated with forelimb dexterity. The remainder of the variation, within carnivorans at least, is likely due to species specific selection pressures. This would suggest that the evolution of complex motor behaviours may be adaptive and therefore may play a significant role in the invasion of some ecological niches. Whether the relationships presented herein will hold true for other mammalian taxa requires further analysis. It may be instructive to conduct similar forms of analyses in other taxa known to possess species with variable levels of forelimb dexterity, particularly the Rodentia, Marsupialia and Primates. Similar patterns across different lineages may not only demonstrate the importance of forelimb dexterity in particular niches, but also may provide useful insight into the morphological bases underlying both high and low forelimb dexterity.

CHAPTER FIVE*

PART I. GENERAL DISCUSSION

The analysis of forelimb dexterity in carnivorans has revealed that several of the factors considered to be important in the elaboration of forelimb dexterity are relatively unimportant. Relative brain size, neocortical volume, gross manus morphology all exhibited non-significant relationships with forelimb dexterity. Arboreal locomotion was significantly correlated with dexterity, but only at the proximal level and accounted for a relatively small percentage of the total variance. In contrast, both phylogeny and diet exhibited significant relationships and accounted for a relatively large percentage of the total variance. In opposition to Gittleman's (1986a) theory, however, the relationship between vertebrate predation and dexterity was negative rather than positive. Thus, the main aim of this study, to ascertain the relative importance of these various factors on the evolution of forelimb dexterity, has been accomplished. Prior to examining this from a more integrative perspective, it is necessary to discuss some of the limitations of the present analysis.

Limitations of Comparative Analyses

The major limitation of any comparative analysis is the data set. The inclusion/exclusion of various taxa or types of data can play a significant role in the outcome and interpretation of the results. An excellent example is the polar bear in both chapters three and four. In both instances, the contrast between the polar bear and its closest relative, the brown bear, was a significant outlier. Despite the fact that its inclusion did not alter the significance of the results, it did alter the proportion of variance explained. Therefore, it could be suggested that the inclusion of additional species may alter the interpretation of the results. There are, unfortunately, few solutions to this problem, particularly when the selection of species is based upon availability. Members of all carnivoran families (Wozencraft 1989) were, however, examined to ensure that the maximum amount of phylogenetic diversity was achieved. Furthermore, preliminary observations, that is less than 2 hours of total observation time, of thirteen additional species indicate that the observed range of dexterity is representative of the order (Table 5.1). The only possible exceptions may be the two-spotted palm civet (*Nandinia binotata*) and the kinkajou (*Potos flavus*) which have both been described to have equal, if not better, manipulatory skills than some primates (Estes 1991; McClearn 1990). Thus, there is a low likelihood that the inclusion of additional species will affect the significance of the results, but qualitative changes in the amount of variance explained cannot be dismissed.

Related to the species composition of the data set is the applicability of the present findings to other mammalian taxa. Many other mammalian taxa are known to contain species which are capable of executing skilled forelimb movements: Chiroptera, Dermoptera, Edentata, Insectivora, Marsupialia, Rodentia, Pholidota, Primates and Scandentia (see below). Similarly, they span broad ranges of neural, morphological and ecological phenotypes. Relative to carnivorans, and each other, they are evolutionarily separated by millions of years (Novacek 1993). Thus, a myriad of combinations and permutations of selective forces have been involved in the evolution of species within each order. As a result, it is possible that the present findings may not be applicable to all mammals. For example, although there was no significant relationship between neocortex and dexterity in carnivorans, there is apparently a significant relationship between neocortex and distal dexterity in marsupials (Iwaniuk et al. in press).

A third limitation may be the dexterity rating system. Although the dexterity

Table 5.1 Dexterity index scores for additional species based upon preliminary observations (less than 2 hours of observation time).

Family	Species		Proximal	Distal	Total
Canidae	*Alopex lagopus*	Arctic fox	1	2	3
	Vulpes vulpes	Red fox	1	2	3
Felidae	*Lynx rufus*	Bobcat	1	3	4
Herpestidae	*Mungos mungo*	Banded mongoose	1	3	4
Mustelidae	*Lutra canadensis*	Canadian river otter	4	5	9
	Martes pennanti	Fisher	3	7	10
	Mellivora capensis	Ratel	5	8	13
	Pteroneura brasiliensis	Giant river otter	4	10	14
	Spilogale putorius	Eastern spotted skunk	5	6	11
	Taxidea taxus	North American badger	4	2	6
	Vormela peregnusa	Marbled polecat	2	3	5
Ursidae	*Helarctos malayanus*	Sun bear	8	12	20
Viverridae	*Viverricula indica*	Lesser Oriental civet	1	0	1

index employed in this thesis is a considerable improvement over those used previously, it may appear limited because only feeding behaviours were observed. An attempt was made to corroborate observations of forelimb usage in feeding with that of other behaviours, for each of the species examined. Forelimb use during both locomotion and grooming was significantly less variable than that during feeding. In three species, the cheetah, polar bear and masked palm civet, patterns of predatory behaviour exhibited slightly different variability in forelimb use (pers obs.; Eaton 1974; Eisenberg and Leyhausen 1972; Savage 1999), but the absence of published reports and/or documentary footage for most of the species precluded the inclusion of predatory behaviour with feeding to measure dexterity. Even so, the dexterity index for these three species would have only been increased by a maximum of 2 or 3 points and did not significantly affect the significance of the results presented.

A fourth limitation is the phylogenetic hypothesis under which the comparative methods were performed. The phylogeny of Bininda-Edmonds et al. (1999) is a type of 'supertree' resulting from the analyses of various separate phylogenetic data sets on the species of interest. Morphological, molecular and chromosomal data are therefore combined to form a matrix of the elements included which is then analysed by a method known as matrix representation with parsimony analyses (MRP) (Baum 1992; Ragan 1992). Although this method often yields trees which are well resolved (e.g. Bininda-Edmonds et al. 1999; Purvis 1995), there are a number of problems inherent in this method such as being node rather than tree-based in determining relationships and placing taxa in positions which they would not occupy with the use of other total evidence analyses (reviewed in Bininda-Edmonds and Bryant 1998). Thus, the position of some species on Bininda-Edmonds et al.'s (1999) carnivoran phylogeny may be questionable.

In the absence of other suitably detailed carnivoran phylogenies, however, the phylogeny used was the best one currently available. Furthermore, relatively minor alterations in the position of individual species in relatively large data sets appears to have little influence on the results of independent contrasts (Iwaniuk, in review; Pellis and Iwaniuk in press; Price 1997).

A final limitation is the comparative methods themselves. All statistical methods are constrained by the assumptions implicit in their application and modern comparative methods are no exception in this regard. For example, independent contrasts, despite being the most statistically powerful and robust method currently available (Diaz-Uriarte and Garland 1998, 1996; Garland et al. 1992, 1993, 1999; Martins and Garland 1991), is limited to the examination of correlated evolution. That is, it cannot determine whether evolutionary changes in one trait cause changes in another trait, but only whether they vary in the same direction over evolutionary time. For this reason, the application of multivariate statistics to independent contrasts data can be problematic. Take, for example, the relationships between arboreality and proximal dexterity and diet and proximal dexterity (see Chapter 4). Independent linear regression of these variables indicated a positive relationship for the former and a negative relationship for the latter. If an equally weighted multiple regression model is applied to this, the result is likely to be non-significant. Another situation can arise when examining the slope of two lines. Because the regression of independent contrasts must be forced through the origin (Garland et al. 1992), the use of ANCOVAs to test for a difference between two lines will only be able to discern slopes (i.e. the interaction effect) and not intercepts. Thus, unless the two groups differ in the rate at which they are related to the independent variable, no effect will be recognised.

Directional methods can address some of these problems and are potentially useful in determining causal relationships (Lindenfors and Tullberg 1998), but they too can be problematic. Many of the directional methods have been criticised recently because of their reliance upon tracing ancestral states, redundancy within the resulting data set and the lack of assurance that 'normal' statistics can be performed on the data (Harvey and Pagel 1991). There is little resolution to the first problem as there is dissension amongst evolutionary biologists as to what forms of parsimony should be used in reconstructing ancestral states in general (see reviews in Cunningham et al. 1998; Omland 1999 and below). The redundancy issue is more easily resolved: any statistics performed can have a modified degrees of freedom such that the statistical effect of redundancy is minimised (Harvey and Pagel 1991). Lastly, the issue of appropriate statistical tests is reliant upon simulation studies, akin to those performed by Garland and colleagues (Diaz-Uriarte and Garland 1998, 1996; Garland et al. 1992, 1993; Martins and Garland 1991), to ascertain the robustness of these methods and the appropriateness of directional techniques.

The most controversial method, however, is the assessment of the phylogenetic component of variation present in a trait. The application of phylogenetic autocorrelation (Cheverud et al. 1985) has been used in a variety of comparative studies (e.g. Gittleman and Van Valkenburgh 1991), but the robustness of this method has been questioned. Martins (1996; Martins and Garland 1991) has found that the method is unreliable at low sample sizes (n < 40) and is highly contingent upon the level at which autocorrelation is tested. That is, determining the phylogenetic distance or taxonomic level at which autocorrelation occurs is crucial to the calculation of the phylogenetic component of trait variance. More recently, the application of eigenvector analysis to the autocorrelation matrix has been shown to be more robust and powerful than autocorrelation alone (Diniz-Filho et al. 1998), but a great deal of skepticism remains (Garland, pers. comm.). One possible solution is to utilise nested ANOVAs of taxonomic levels (Harvey and Pagel 1991) as shown in Chapter 4. Although this method is dependent upon a detailed taxonomy of the species being studied, it would appear to be less fraught with confusion and uncertainty than phylogenetic autocorrelation. The application of a nested ANOVA to the carnivoran data set did not, however, appreciably alter the results (Table 4.3). Thus, in this instance, the use of phylogenetic autocorrelation yielded similar results to other methods of estimating the phylogenetic component of interspecific variation.

The Comparative Analysis of Motor Patterns

To date, there have been few examinations of non-display behaviours using modern comparative techniques. Although not explicitly stated in the literature, the reason appears to be that it has been assumed that such behaviours are difficult, if not impossible, to homologise which makes understanding their evolution impracticable. The results presented herein indicate, however, that motor behaviours can be homologised to the same extent as displays or related behaviours. This is not to say that they can potentially be used as characters in a cladistic analysis, as there are numerous instances of convergence (e.g. snow-adapted carnivorans), but that there does appear to be a phylogenetic component to motor behaviours.

One of the ramifications of these findings is that the examination of motor behaviours, and their correlates, requires a phylogenetic framework. For example, Godfrey et al. (1991) examined articular surface area of the humerus and femur of variously inter-related mammals in an attempt to understand the relationship between joint surface area and locomotion. They, however, performed their analysis without a phylogenetic context. Given that they compared various groups of primates to carnivorans, it is difficult to ascertain whether they would have achieved the same result had they incorporated phylogenetic information. Similarly, Harris and Steudel (1997) and Jones and Stoddart (1998) examined locomotion and hindlimb proportions in carnivorans and dasyurid marsupials respectively without addressing phylogenetic constraints. The point is that to ensure that a comparative analysis is as robust as possible, it is necessary to utilise modern comparative techniques at some level. Failure to do so may result in defining apparent relationships between structure and function which are significantly confounded by phylogenetic effects.

The results also demonstrate that analyses of motor behaviour evolution and diversification can be important tools in understanding the mechanics of behavioural evolution. Since most other studies have focussed upon displays or similar behaviours, the evolution of different behaviours is often discussed in terms of speciation or sexual selection. The result of this myopic perspective is that it ignores the different mechanics involved in the evolution of more labile behaviours, such as forelimb dexterity. Unlike display behaviours, the differentiation of forelimb dexterity appears to occur at multiple points throughout carnivoran, and to some extent, mammalian phylogeny. For example, major changes occur early in carnivoran evolution which, in part, determine the forelimb dexterity of descendant species, as shown by phylogenetic autocorrelation. Major changes can also occur further down the phylogeny at species branch tips.

Implications for the Evolution of Dexterity

As discussed in the preceding chapters, the various correlates exhibited varying patterns and degrees of correlation with each of the three dexterity scores. The most influential of these effects appears to be vertebrate predation, with phylogeny and arboreality exhibiting lesser effects. It would appear then that high degrees of forelimb dexterity are more likely to occur in omnivorous, arboreal species within the caniform lineage (see Chapter 4). Low degrees of forelimb dexterity are therefore more likely to occur in predatory, terrestrial species within the feliform lineage. Intermediate forms are then scattered throughout varying dietary and locomotory specialisations and within each of the carnivoran suborders.

Based upon this pattern, a model can be derived in which one can trace the pattern of forelimb dexterity diversification along the carnivoran phylogeny. Beginning with a miacid-like ancestor which was somewhat predatory, moderately arboreal, and possessed an intermediate level of dexterity, forelimb dexterity tended to increase among the caniforms and decrease among the feliforms. As members within each lineage invaded new niches and became more ecologically specialised, the degree of dexterity then increased or decreased according to the specific trade-offs between locomotor demands and the use of the forelimbs during non-locomotory activities. This diversification continued to occur all the way to the terminal branches; appearing as 'idiosyncratic' increases/decreases in forelimb dexterity. Thus, the progressive invasion of novel niches is accompanied by a corresponding diversification of forelimb dexterity.

This pattern suggests that the differential evolution of forelimb dexterity may be a key component to the invasion of a novel niche. That is, to take advantage of available resources, the degree of specialisation of the forelimbs for locomotion or manipulation may be modified to permit a member of a lineage to occupy a niche novel to other lineage members. One example of this is the invasion of the bamboo feeding niche by the giant panda. The panda's ability to manipulate bamboo culms in a variety of ways may have increased its bamboo processing efficiency such that it was able to invade a niche not previously occupied. Similarly, the decrease in forelimb dexterity of the snow leopard, and presumably an increase in the reliance upon efficient locomotion, may be advantageous for a large predator in a hostile environment

Similar evolutionary scenarios can be depicted for every species examined, but the point is that forelimb dexterity appears to play a crucial role in the ability of a species to invade a novel niche. This is likely due to the fact that forelimb dexterity can affect handling time in ecological models of optimal prey choice. For example, if one considers the equation determining prey choice in Krebs and Davies (1993) (Equation 5.1), variations in handling time determine net energy gain and therefore affect prey choice.

Equation 5.1:

$$\frac{E_1}{S_1 + h_1} > \frac{E_2}{S_2 + h_2}$$

where 'E' is the energy value, 'S' is searching time and 'h' is handling time for two different prey items ($_1$ and $_2$).

The side of the equation with the largest value (net energy gain) should be the food item of choice by a predator. If one assumes that with higher dexterity a species can handle food items more efficiently and effectively, then there should also be a decrease in handling time. Species with higher forelimb dexterity may then be able to reduce the size of the denominator and receive a relatively larger energy return per food item than species with lower dexterity and equal foraging times. This would potentially increase the number of food choices available to highly dexterous species and allow them to exploit novel resources. The giant panda feeding on nutrient-poor bamboo serves as an example of just such an evolutionary scenario.

Based upon optimal prey choice and the negative correlation between vertebrate predation and forelimb dexterity, a series of predictions can be made concerning the likely patterns of forelimb dexterity evolution. Firstly, species which occupy a novel niche relative to closely related species, should undergo a marked change in forelimb dexterity. The direction of this change is dependent upon a host of specific ecological variables, but nonetheless appears to be present (see pantherids and ursids in Chapter 4). Within the carnivoran species which have not been examined, I would predict that similar changes may occur in the semi-aquatic mink (*Mustela vison*) relative to other *Mustela* species. In other taxa, such as marsupials, major changes in forelimb dexterity would be likely to occur in the scansorial rock ringtail possum (*Petropseudes dahli*) relative to its arboreal relatives (*Pseudocheirus* spp. and *Hemibelideus lemuroides*). Similarly, in primates a large change in forelimb dexterity is likely to occur between the bamboo eating gentle lemurs (*Hapalemur* spp.) and their closest relative, the ring-tailed lemur (*Lemur catta*) (Purvis 1995).

A second prediction is that species with the broadest feeding niche should possess the highest forelimb dexterity. Although there are obvious exceptions to this (e.g. canids, the giant panda), it appears to be applicable as a general rule within mammals. For example, within marsupials, browsing macropods tend to have higher forelimb dexterity than grazing forms (Iwaniuk, 1997). Similarly, omnivorous carnivorans tend to have higher forelimb dexterity than other forms (see Chapter 4). Bishop's (1964) study of primate forepaw use also supports this general trend. Predatory species, such as bushbabies and lorises, had more stereotypical reaching and grasping movements and less behavioural plasticity than more omnivorous taxa such as lemurs and simians. Lastly, the relationship between feeding niche and dexterity is supported by comparative studies of rodents in which rats possess better seed handling skills than other muroid and sciurid rodents which have been studied (Whishaw et al. 1998). I predict that not only will this relationship persist in other species of marsupials, carnivorans, primates and rodents, but that this pattern may also be found in presently unstudied taxa such as edentates (sloths, anteaters) and insectivores.

PART II. THE ORIGINS OF SKILLED FORELIMB MOVEMENTS

These correlates of forelimb dexterity are helpful in understanding the diversification of skilled forelimb movements in mammals, and particularly in carnivorans, but they do little to contribute to our understanding of where or when skilled forelimb movements first arose. To accomplish this, a broader perspective is required as well as a working definition of homology (see reviews in Panchen 1994 and Rieppel 1994). For the purposes of the present analysis, I will use Mayr's (1982) definition of homology and treat skilled forelimb movements as homologous if they can be traced continuously back to a common ancestor. This is the same definition which has been used in both behavioural (Greene 1994) and neural (Striedter and Northcutt 1991) studies.

To determine whether skilled forelimb movements are homologous across tetrapods, it is therefore necessary to trace their presence along a phylogeny. Based upon my own *ad hoc* observations at various zoological institutions during the course of my thesis research, personal communications with various researchers (G.M. Burghardt, S.M. Pellis) and published reports on grasping, I scored 29 different tetrapod taxa as having/not having skilled forelimb movements (Table 5.2). Only those species for which actual prehension was observed or reported scored a presence (i.e. a '1'). Taxa for which the presence of skilled forelimb movements were unknown were scored such that a value of '0' was equally likely as a '1' (i.e. equivocal). Scoring taxa like this, however, precludes many species from scoring a presence of skilled forelimb movements because they lack independent digits to grasp objects. Therefore, a second set of presence/absence scores

Table 5.2. The presence or absence of skilled forelimb movements in various tetrapod taxa.

Class		Skilled forelimb movements[a]	Rudimentary skilled forelimb movements[c]	References[d]
Amphibia	Gymniophona	0	0	—
	Urodela	0/1	0/1	—
	Anura	1	1	Gray et al. 1997
Archosauria	Crocodylia	1	1	juvenile crocodiles (*Crocodylus porosus*), pers. obs.
	Aves	0[b]	0	—
	Sphenodontia	0/1	0/1	—
	Sauria	1	1	Burghardt, pers. comm.; Auffenberg 1981
	Serpentes	0	0	—
	Chelonia	0	1	Burghardt, pers. comm.
Mammalia	Monotremata	0	0	—
	Marsupialia	1	1	Iwaniuk et al. 1999
	Edentata	1	1	Taylor 1985
	Insectivora	1	1	star-nosed mole (*Condylura cristata*), pers. obs.
	Chiroptera	1	1	tent-building bat (*Uroderma* spp.), fruit bats (*Pteropus* spp.), pers. obs.
	Scandentia	1	1	Bishop 1964
	Dermoptera	1	1	McDonald 1984
	Primates	1	1	Bishop 1964
	Hyracoidea	0	0	—
	Sirenia	0	1	*Trichechus* spp., pers. obs.
	Proboscidea	0	0	—
	Tubulidentata	0	0	—
	Macroscelidea	0	0	—
	Rodentia	1	1	Whishaw et al. 1998a

Lagomorpha	0	0	—
Artiodactyla	0	0	—
Cetacea	0	1	*Tursiops truncatus*, pers. obs.
Perissodactyla	0	0	—
Pholidota	1	1	Grzimek 1990
Carnivora	1	1	present study

[a] the presence of all aspects of skilled forelimb movements, reaching, grasping and manipulation, is scored as follows: '0' - absent, '1' - present, and '0/1' - unknown.

[b] only one bird species, the hoatzin (*Opisthocomus hoatzin*), is known to grasp with its forelimbs when young.

[c] under this classification of skilled forelimb movements, grasping with the digits does not necessarily occur. Thus, only reaching and manipulation appear to be present. It was scored as follows: '0' - absent, '1' -present, and '0/1' - unknown.

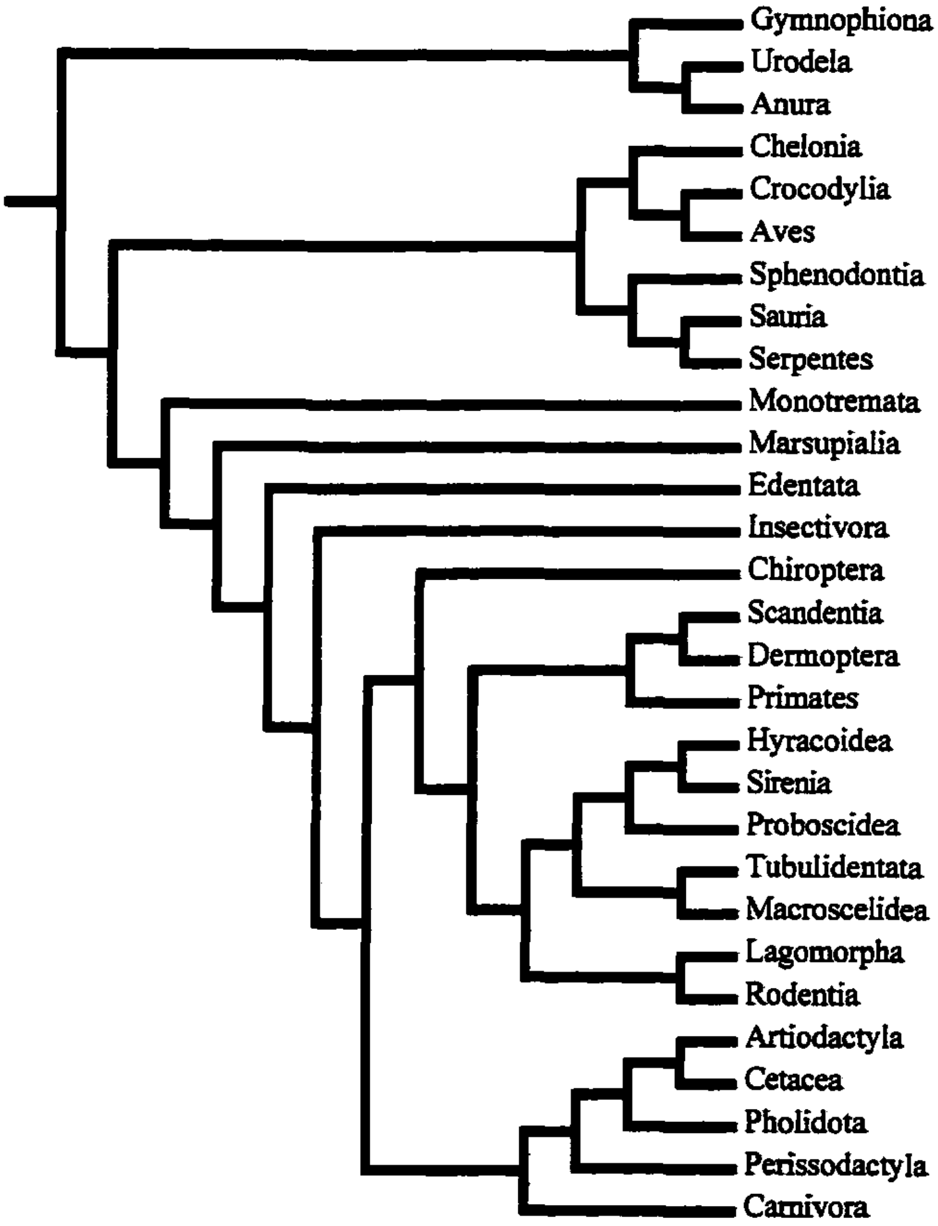
[d] references are given for those species which scored a '1' on either of the skilled forelimb movement categories

were given whereby those species which execute the basic aspects of skilled forelimb movements (e.g. reaching and manipulating items without grasping, or grasping and manipulation without reaching) scored a presence. For example, directing food into the mouth with the forefoot in aquatic turtles, holding beach balls between flippers in bottle-nosed dolphins (*Tursiops truncatus*) or shovelling food into the mouth with the flippers in manatees (*Trichechus spp.*) all scored a presence.

A phylogeny of the various groups was reconstructed based upon a variety of recent studies on tetrapod evolution (Hedges and Poling 1999; Kirsch and Mayer 1998; Liu and Miyamoto 1999; Mindell et al. 1999) (Figure 5.1). Although the arrangement of some taxa (e.g. interordinal relationships within Mammalia) may be questionable (Liu and Miyamoto 1999), it is important to note that different arrangements (e.g. Arnason et al. 1997; Novacek 1993; Shoshani and McKenna 1998) gave the same results reported below.

A number of different algorithms are currently available for determining the most likely ancestral states of reconstructed characters (Cunningham et al. 1998; Omland 1999; Pagel, 1999). I employed two different methods in determining where skilled forelimb movements first arose and whether it is homologous across tetrapods. Firstly, maximum parsimony, that is the hypothesis requiring the fewest changes along the phylogeny (Futuyma 1986), was employed. This method is the simplest form of character mapping and has been used in previous examination of brain-behaviour relationships (Gray et al. 1997; Nishikawa 1997). It can be, however, problematic for a number of reasons. For example, parsimony, by definition, assumes that gains and losses are equally likely in evolution. Therefore, an additional model of ancestral character reconstruction were employed: unequal weightings. This assumes that skilled forelimb movements are more

Figure 5.1: A phylogeny of the major tetrapod taxa based upon the phylogenies in: Hedges and Poling (1999), Kirsch and Mayer (1998), Liu and Miyamoto (1999) and Mindell et al. (1999).


Gymnophiona
Urodela
Anura
Chelonia
Crocodylia
Aves
Sphenodontia
Sauria
Serpentes
Monotremata
Marsupialia
Edentata
Insectivora
Chiroptera
Scandentia
Dermoptera
Primates
Hyracoidea
Sirenia
Proboscidea
Tubulidentata
Macroscelidea
Lagomorpha
Rodentia
Artiodactyla
Cetacea
Pholidota
Perissodactyla
Carnivora

easily lost than gained. Although this is little different from assuming that there are equal probabilities of both (Omland 1999), there is support for such an assumption in the range of studies have shown that losses occur more frequently than gains (Cunningham et al. 1998; Hart et al. 1997; Lee and Shine 1998; Omland 1997, 1999; Price and Birch 1996). Furthermore, given that losses of skilled forelimb movements appear to be related to marked changes in forelimb morphology (e.g. fusion of digits) and there are no known examples of such species which have regained skilled forelimb movements, it would appear that this assumption is quite likely.

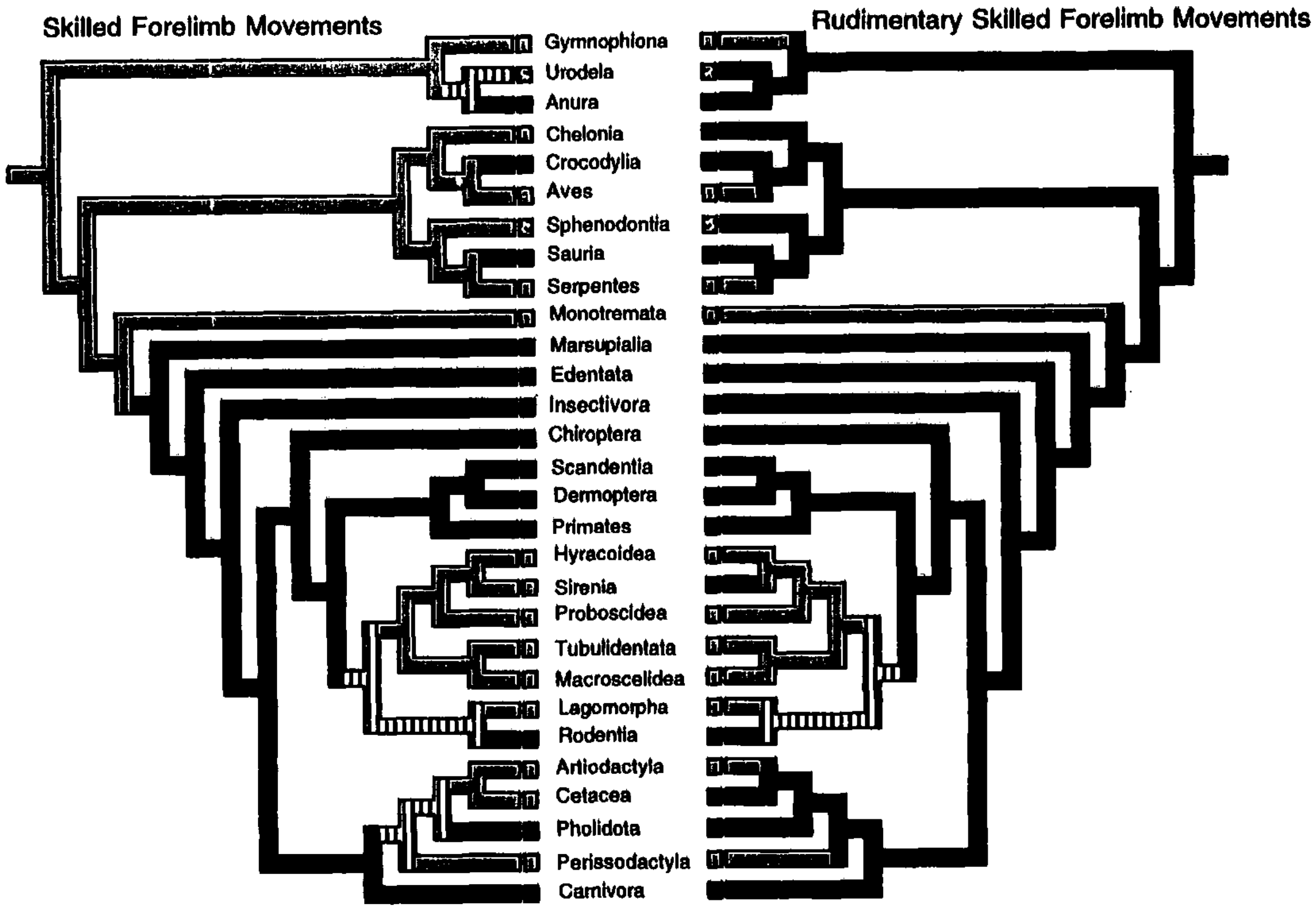
The character mapping program MacClade v. 3.05 (Maddison and Maddison 1992) was used to trace characters using the first two models of evolutionary change. For the unequal change model, losses were assumed to be twice as likely as gains. Increases from 1.5 to 5 times produced identical results, so only the two-fold results will be presented.

Maximum Parsimony Model

Mapping of skilled forelimb movements using maximum parsimony yielded an ancestral state of '0' for the base of the tree (Figure 5.2a). That is, the presence of skilled forelimb movements was absent at the base of the tetrapod phylogeny. Similarly, the bases of the Amphibia, the 'reptiles' and Mammalia indicate a lack of skilled forelimb movements. Within mammals, after the branching of the monotremes, the ancestral state of the eutherian mammals is that of presence of skilled forelimb movements.

When the presence of rudimentary skilled forelimb movements was mapped onto the tetrapod phylogeny, marked differences were found. For example, the state of the base of the tree was was presence of skilled forelimb movements, rather than absence (Figure 5.2b). The bases of the Amphibia, 'reptiles' and Mammalia also indicated that

Figure 5.2: Character mapping of the presence/absence of **a)** skilled forelimb movements and **b)** rudimentary skilled forelimb movements across the major tetrapod taxa assuming that evolutionary losses are as likely as gains (i.e. maximum parsimony) (data from Table 5.2).



Skilled Forelimb Movements

Rudimentary Skilled Forelimb Movements

the presence of rudimentary skilled forelimb movements was the most parsimonious state. This suggests that skilled forelimb movements in frogs and mammals are homologous and that losses, rather than gains, have independently occurred throughout tetrapod evolution.

Unequal Gains and Losses

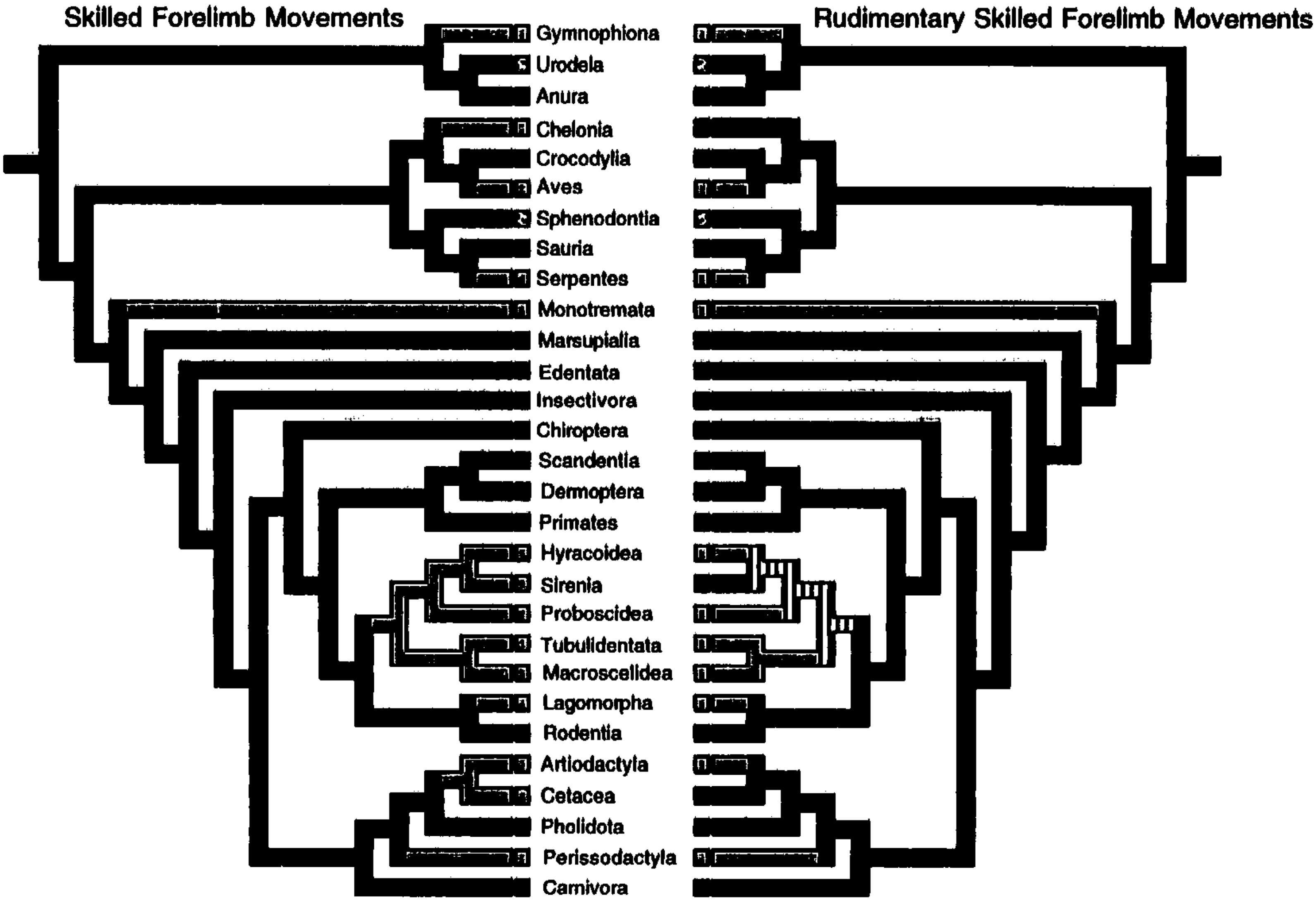
With the application of the unequal model (i.e. losses more likely than gains) to skilled forelimb movements, the ancestral state of the tree was also presence of skilled forelimb movements (Figure 5.3a). All of the nodes were resolved and most of them were in a state of presence of skilled forelimb movements. The only exceptions were the divergence between the even-toed ungulates (Artiodactyla) and the whales (Cetacea) and the clade containing the elephants (Proboscidea), manatees (Sirenia), hyraxes (Hyracoidea), elephant shrews (Macroscelidea) and the aardvark (Tubulidentata). For both of these groups, the ancestral state was absence.

A virtually identical pattern was produced when the rudimentary skilled forelimb movement scores were mapped (Figure 5.3b). Again, the ancestral state of most clades was presence. The only exception was the clade containing the elephants, manatees, hyraxes, elephant shrews and the aardvark which was equivocal. This is due to the presence of reaching and manipulation in manatees.

Are Skilled Forelimb Movements Wiping or Scooping?

The present analysis and review suggests that skilled forelimb movements are an 'ancestral' feature of mammals and, possibly, tetrapods which has its origins relatively early in evolutionary history. Although this is not proof of homology in skilled forelimb movements, it certainly implies that homology is more likely than homoplasy. One intriguing question which arises from this analysis is: what are skilled forelimb

Figure 5.3: Character mapping of the presence/absence of **a)** skilled forelimb movements and **b)** rudimentary skilled forelimb movements across the major tetrapod taxa assuming that evolutionary losses are twice as likely as gains (data from Table 5.2). Note that the results were the same when losses were between 1.5 and 5 times as likely as gains as well.


Skilled Forelimb Movements
Rudimentary Skilled Forelimb Movements
Gymnophiona
Urodela
Anura
Chelonia
Crocodylia
Aves
Sphenodontia
Sauria
Serpentes
Monotremata
Marsupialia
Edentata
Insectivora
Chiroptera
Scandentia
Dermoptera
Primates
Hyracoidea
Sirenia
Proboscidea
Tubulidentata
Macroscelidea
Lagomorpha
Rodentia
Artiodactyla
Cetacea
Pholidota
Perissodactyla
Carnivora

movements derived from? Bracha et al. (1990) suggested that skilled forelimb movements are derived from digging behaviour in rats. Grillner and Wallen (1985), on the other hand, suggests that they are simply an exaggeration of a stepping motion in locomotion. A close examination of forelimb movements involved in reaching and grasping prey in anurans, however, suggests a different origin.

Anurans, possess 5 different types of forelimb usage patterns according to Gray et al. (1997): 1) scooping - digits are splayed and back of the hand pushes food into the mouth; 2) wiping - the palm pushes protruding prey towards the midline; 3) prey stretching - hands hold prey down as mouth pulls it upward; 4) grasping - digits wrap around prey and transport it into the mouth; and 5) grasping with rotation - wrist rotates following the grasp such that the palms are oriented towards the mouth. The last two categories correspond to the definition of skilled forelimb movements used in the present study. The first three, however, offer plausible alternative to Bracha et al.'s (1990) and Grillner and Wallen's (1985) proposed origins of skilled forelimb movements.

Prey stretching is unlikely to be the ancestral form of skilled forelimb reaching because of its use in a small number of frogs. The sporadic occurrence of prey stretching suggests that it is a derived behaviour, possibly related to some aspect of their ecology. For example, Gray et al. (1997) suggest that it may be important in predation of noxious prey.

The two alternatives, scooping and wiping, therefore, seem to be the most likely candidates for a progenitor behaviour of skilled forelimb movements. It is difficult to assess which one of these is the most likely candidate, as they are both widespread across anurans. If one assumes that the more simplistic motor pattern is the ancestral form, then scooping seems to be the most appropriate choice. Wiping involves bringing the forelimb upwards, rotation and finally contact with the prey item, whereas scooping does not involve a rotatory element. On the other hand, wiping is occasionally present as part of the feeding repertoire in salamanders (*Ambystoma* spp.) (pers. obs.) indicating that its presence in frogs may be an ancestral feature of amphibians. Ultimately, the answer to the question of whether scooping or wiping is the ancestral motor pattern from which skilled forelimb movements are derived is dependent upon detailed kinematic and developmental studies in amphibians. It is, however, apparent that skilled forelimb movements are more likely to be descended from scooping or wiping than digging (Bracha et al. 1990) or stepping (Grillner and Wallen 1985).

Implications for the Evolution of the Motor System

Skilled forelimb movements appear to have originated early in tetrapod evolution, possibly as early as the divergence between amphibians and amniotes. At the very least, it is an ancestral feature of mammals dating back to the monotreme-eutherian divergence (at least 70 millions years ago) (Kirsch et al. 1997). This suggests that various aspects of the nervous system which have traditionally been considered to be integral to the execution of skilled forelimb movements are not required. For example, the corticospinal tract (CST) has been suggested to be a critical descending pathway from the brain to the execution of skilled forelimb movements (Heffner and Masterton 1983, 1975). Both the depth of penetration into the spinal cord and length of the fibres were suggested to be positively correlated with forelimb dexterity. More recently, I performed an independent contrasts analysis on these same characters and found that length, but not depth, are significantly correlated with forelimb dexterity (Iwaniuk et al. 1999a). The present analysis indicates, however, that even species devoid of a CST may be capable of performing skilled forelimb movements. Frogs (Anura) are capable of not only grasping prey, but also wrist rotation and placement of prey items into the mouth (Gray et al. 1997), yet they lack a CST (Butler and Hodos 1996). Corroborating evidence can be found in numerous CST lesion studies in which skilled forelimb movements were impaired, but not ablated (Kuypers et al. 1976; Lawrence and Kuypers 1968; Passingham et al. 1983; Schwartzman 1978; Whishaw et al. 1993; Whishaw et al. 1998). This suggests that the CST may not be required for skilled forelimb movements to occur.

An alternative descending pathway is the rubrospinal tract (RST). The RST is present in all tetrapods, with the exception of gymnophiones and snakes, and has been suggested to be related with the presence of limbs or limb-like structures (Butler and Hodos 1996). On the basis of CST lesion studies, Kuypers et al. (Kuypers 1964, 1981; Kuypers et al. 1976; Lawrence and Kuypers 1968) proposed that the RST may be capable of replacing CST input to control forelimb movements. Three pieces of evidence indicate that the RST may not be required for skilled forelimb movements to occur either. Firstly, the ray (*Raja clavata*) has a rubrospinal tract, but lacks forelimbs (Smeets and Timerick 1981); secondly, it is present in many tetrapod species which do not execute skilled forelimb movements ; and lastly, sectioning of the rubrospinal tract does not affect whether animals can reach or not (McKenna and Whishaw prelim. data; Pettersson et al. 1997). Furthermore, damage to the red nucleus affects performance in a similar manner to CST lesions, but does not cause complete loss of skilled forelimb movements either (reviewed in Whishaw et al. 1998). This should not be taken as evidence that there are no descending pathways responsible for skilled forelimb movements, but that neither of these lateral pathways are absolutely necessary for the movements to occur.

Another group of descending pathways which may be important in the execution of skilled forelimb movements are the medial pathways. For example, the tectospinal tract appears to be part of the main route of control of motor neurons in reptiles (Butler and Hodos 1996). Similarly, the reticulospinal tract plays an active role as part of the reticular formation in controlling limb and trunk musculature (Butler and Hodos 1996). Both of these medial pathways also appear to affect the performance of skilled forelimb movements (Pettersson et al. 1997; Pettersson 1990). However, independent sectioning of either of these pathways does not abolish skilled forelimb movements.

Since lesions to any of these four descending pathways significantly affects the performance of skilled forelimb movements, but not their presence, it appears likely that the four pathways act synergistically to mediate skilled forelimb movements. That is, signals to the forelimbs are conducted via all four pathways and combine to execute skilled forelimb movements. In the absence of one of the pathways, control over the movements is impaired (e.g. Pettersson et al. 1997), but the movements themselves are still present. Similarly, in those species which do not possess one of the pathways (e.g. CST in anurans), control would appear to be mediated by the remaining descending pathways. Supporting evidence for this theory can be found in a study on reaching in cats by Pettersson et al. (1997) where various combinations of sections were performed with little effect upon whether forelimb movements were executed or not. Presumably, transection of all four pathways would lead to a complete ablation of skilled forelimb movements, but at present this critical experiment has not been reported.

CONCLUSIONS

There is still much to be known regarding skilled forelimb movements. This thesis should be taken as a template of investigating this motor pattern in both mammalian and non-mammalian taxa. Within carnivorans, it appears that only diet and, to a lesser extent, arboreality and phylogeny are reliable predictors of forelimb dexterity. To fully understand these results, however, it is necessary to determine whether the relationships described herein are present/absent in a similar fashion in other mammalian and tetrapod taxa. Once this has been performed, one can begin to ask more specific questions concerning the differential evolution of forelimb dexterity and gain insight into the mechanisms involved. Only at this point, will we begin to understand the relative importance of aspects of the motor system and musculo-skeletal morphology on the execution of forelimb movements.

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Appendix 1. The number of individuals observed (N), scores for proximal, distal and total forepaw dexterity (maximum possible score in brackets), relative brain size, metacarpal-phalanx ('MCP') ratio, average body weight, degree of arboreality ('Arboreality'), relative amount of vertebrate matter in the diet ('Diet') for the carnivore species examined.

Family	Species		N	Proximal dexterity[a] (8)	Distal dexterity (13)	Total dexterity (21)	Brain size[b]	MCP ratio[c]	Body weight[d] (kg)	Arboreality[e]	Diet[f]
Ailuridae											
	Ailurus fulgens	Red panda	7	7	13	20	0.159	—	4.5	3	0
Canidae											
	Canis familiaris	Domestic dog	3	2	3	5	0.094	2.700	30	0	2
	Chrysocyon brachyurus	Maned wolf	4	1	2	3	0.150	4.000	21.5	0	2
	Fennecus zerda	Fennec fox	2	1	2	3	0.024	—	1.3	1	2
	Speothos venaticus	Bush dog	1	1	0	1	0.031	1.923	6.5	0	3
Felidae											
	Acinonyx jubatus	Cheetah	8	1	0	1	-0.129	2.354	53.5	0	3
	Caracal caracal	Caracal	3	1	3	4	-0.005	2.124	16	1	3
	Felis margarita	Sand cat	2	1	3	4	—	—	2	1	3
	Felis nigripes	Black-footed cat	2	1	3	4	-0.009	—	1.8	1	3
	Felis silvestris ornatus	Indian desert cat	3	1	3	4	0.063	—	5.5	1	3
	Leopardus geoffroyi	Geoffroy's cat	2	3	4	7	—	—	4.5	1	3
	Leopardus pardalis	Ocelot	1	8	8	16	0.014	2.084	13.6	2	3
	Lynx canadensis	Canadian lynx	6	1	0	1	0.110	1.604	11.2	1	3
	Panthera leo	Lion	6	6	7	13	-0.080	2.329	156	1	3
	Panthera onca	Jaguar	3	8	9	17	-0.095	1.821	105	2	3
	Panthera pardus	Leopard	3	6	7	13	-0.040	1.867	101	2	3
	Panthera tigris	Tiger	4	6	7	13	0.007	2.072	222.8	1	3
	Panthera uncia	Snow leopard	2	3	4	7	-0.013	1.700	50	1	3
	Prionailurus bengalensis	Leopard cat	7	3	9	12	-0.084	—	5	2	3
	Prionailurus rubiginosa	Rusty-spotted cat	2	1	3	4	0.080	—	2	1	3[g]
	Prionailurus viverrinus	Indian fishing cat	4	3	10	13	0.003	1.950	10.9	1	3[g]
	Puma concolor	Cougar	4	7	10	17	-0.038	2.140	81.5	2	3
Herpestidae											

	Helogale parvula	Dwarf mongoose	2	1	3	4	-0.083	—	0.5	1	1
	Suricata suricatta	Meerkat	5	1	3	4	-0.010	—	0.9	1	1
Hyaenidae											
	Crocuta crocuta	Spotted hyaena	3	1	0	1	-0.048	2.956	63	0	3
	Hyaena brunnea	Brown hyaena	2	1	0	1	-0.068	—	42.3	0	2
Mustelidae											
	Aonyx cinerea	Asian small-clawed otter	2	8	12	20	0.107	—	3	0	0
	Eira barbara	Tayra	2	3	5	8	0.061	1.293	4.5	3	2
	Enhydra lutris	Sea otter	3	5	11	16	0.117	—	38.5	0	0
	Gulo gulo	Wolverine	3	3	5	8	0.155	1.843	19.5	1	3
	Martes americana	American pine marten	5	3	9	12	0.133	2.109	1.1	2	2
	Mephitis mephitis	Striped skunk	6	5	10	15	-0.319	2.206	1.6	0	0
Procyonidae											
	Nasua narica	Coati	6	6	10	16	-0.052	1.887	4.5	3	2
	Procyon lotor	Raccoon	7	8	13	21	0.019	1.952	7	3	1
Ursidae											
	Ailuropoda melanoleuca	Giant panda	1	8	13	21	0.012	1.806	117.5	2	0
	Tremarctos ornatus	Spectacled bear	2	8	12	20	—	1.640	126	2	0
	Ursus americanus	American black bear	5	8	12	20	-0.076	1.838	205	2	0
	Ursus arctos	Brown bear	6	8	12	20	0.074	2.033	287	1	1
	Ursus maritimus	Polar bear	4	2	0	2	0.006	1.875	550	0	3
	Ursus thibetanus	Asiatic black bear	2	8	12	20	0.180	1.521	131.5	2	1
Viverridae											
	Arctictis binturong	Binturong	2	7	7	14	-0.135	1.371	11.5	3	1[g]
	Cryptoprocta ferox	Fossa	1	7	8	15	-0.190	1.600	9.5	3	3
	Genetta genetta	Common genet	2	2	0	2	-0.127	1.769	2	3	3
	Genetta maculata	Forest genet	1	2	0	2	—	—	2	3	3[g]
	Paguma larvata	Masked palm civet	2	1	0	1	0.001	2.105	4.3	3	1[g]

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[a] the scores for proximal, distal and total dexterity were calculated from the dexterity taxonomy (see Figure 2.1). The maximum possible score is shown in brackets.

[b] brain size residuals calculated from data in Gittleman (1986a).

[c] derived from data in Davis (1964), Iwaniuk et al. (in press) and Van Valkenburgh (1985, 1987).

[d] average body weights were obtained from Nowak (1991), except for three felids (*Felis margarita*, *Leopardus geoffroyi*, and *Prionailuurs rubiginosa*) which were taken from alternate sources (Guggisberg 1975 and Johnson and Franklin 1991) and the domestic dog (*Canis familiaris*) which was obtained from the average body weight of the three individuals observed. Where extreme variation in body size according to geographical races occurred (i.e. *Panthera pardus* and *P. tigris*, *Prionailurus bengalensis*, *Ursus arctos*), the average of all of the subspecies was taken as the species average.

[e] references for arboreality are as follows:

[f] references for diet are as follows: Ackerman et al. (1984), Bekoff (1975), Bisbal (1986), Branch (1995), Brosset (1968), Clark et al. (1987), Clevenger (1996), Delibes et al. (1989), Doolan and McDonald (1996), Eaton (1972), Elliott et al. (1977), Emmons (1988), Estes (1980), Ewer (1963), Gompper (1995), Goodman et al. (1997), Grobler (1981), Guggisburg (1975), Haglund (1968), Hamer et al. (1991), Hart et al. (1996), Herrero (1972), Holcroft and Herrero (1991), Hornocker (1972), Hornocker and Hash (1980), Husson (1978), Inoue (1972), Johnson and Franklin (1991), Karanth and Sunquist (1995), Kaufmann (1962), Kaufmann and Kaufmann (1965), Kingdon (1977), Kleiman (1983), Köncke and Leonhardt (1986), Konecny (1989), Kruuk et al. (1994), Kruuk and Turner (1967), Laborde (1986a, b), Langguth (1975), Lay et al. (1970), Leach (1977a, b), Lekagul and McNeely (1977), Lotze and Anderson (1979), McClearn (1992), Mills (1989, 1990), Mills and Mills (1978), Mondolfi (1982, 1989), Mondolfi and Hoogersteijn (1982), Motta-Junior et al. (1996), Nellis et al. (1972), Nesbitt (1975), Nowak (1991), Oli (1993), Parker et al. (1983), Pearson (1975), Peres (1991), Peyton (1980), Rabinowitz (1990), Rabinowitz and Nottingham (1986), Rasa (1973, 1977), Reid et al. (1991), Renous et al. (1998), Ruggiero (1991), Russell (1975), Schaller (1967, 1972, 1977), Schaller et al. (1989), Schaller and Vasconcelos (1978), Schwartz and Franzmann (1991), Seidensticker and McDougal (1993), Servheen (1983), Sharma (1979), Smithers (1971), Stirling and Archibald (1977), Sunquist et al. (1989), Taber et al. (1997), Tarasoff et al. (1972), Taylor (1070, 1972, 1989, Thompson and Colgan (1990), Turnbull-Kemp (1968), Verts (1967), Wade-Smith and Verts (1982), Wemmer (1977), Whitney and Underwood (1952), Wright et al. (1997), Yanosky and Mercolli (1994), Zielinski et al. (1983).

[g] studies of actual diet (i.e. stomach or fecal analysis) could not be found for these species and therefore their diet score is an estimate based upon available anecdotal literature.

Appendix 2. The individual scores for each of the 22 categories of the dexterity index (Figure 2.1).

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14[a]	15	16	17	18	19	20[b]	21[c]	22[d]
Ailurus fulgens	1	1	1	1	1	2	1	1	1	1	1	1	0	0	2	0	1	1	1	1	1	0
Canis familiaris	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0
Chrysocyon brachyurus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Fennecus zerda	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Speothos venaticus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acinonyx jubatus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Caracal caracal	0	0	1	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Felis margarita	0	0	1	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Felis nigripes	0	0	1	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Felis silvestris ornata	0	0	1	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Leopardus geoffroyi	0	0	1	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	1	0	0
Leopardus pardalis	2	1	1	1	1	2	1	1	1	1	0	1	0	0	1	0	0	0	0	1	1	0
Lynx canadensis	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Panthera leo	1	1	1	1	1	1	1	0	0	1	0	1	0	0	1	1	0	1	0	1	0	0
Panthera onca	2	1	1	1	1	2	1	0	0	1	0	1	0	0	1	1	0	1	0	1	0	0
Panthera pardus	1	1	1	1	1	1	1	0	0	1	0	1	0	0	1	1	0	1	0	1	0	0
Panthera tigris	1	1	1	1	1	1	1	0	0	1	0	1	0	0	1	1	0	1	0	1	0	0
Panthera uncia	1	0	1	0	0	1	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0
Prionailurus bengalensis	0	1	1	0	0	1	1	1	1	1	0	1	0	0	1	1	0	0	0	1	1	0
Prionailurus rubiginosa	0	0	1	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Prionailurus viverrinus	0	1	1	0	0	1	1	1	1	1	0	1	0	0	1	1	0	0	0	1	1	0
Puma concolor	1	1	1	1	1	2	1	1	1	1	0	1	0	0	1	1	0	1	0	1	1	0
Helogale parvula	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0
Suricata suricatta	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0
Crocuta crocuta	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hyaena brunnea	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aonyx cinerea	2	1	1	1	1	2	1	1	1	1	1	0	0	0	2	1	1	1	0	1	0	1
Eira barbara	0	1	1	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0
Enhydra lutris	0	1	1	1	1	1	1	1	0	1	0	0	0	0	2	1	1	1	1	1	0	1
Gulo gulo	1	1	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0
Martes americana	1	0	1	0	0	1	1	0	1	1	1	1	0	0	1	0	0	0	1	1	1	0
Mephitis mephitis	0	1	1	1	1	1	1	1	0	1	1	1	0	0	2	0	0	0	1	1	1	0
Nasua narica	1	1	1	1	1	1	1	1	1	1	1	1	0	0	2	0	0	0	0	1	1	0
Procyon lotor	2	1	1	1	1	2	1	1	1	1	1	0	0	0	2	1	1	1	0	1	1	1
Ailuropoda melanoleuca	2	1	1	1	1	2	1	1	1	1	1	0	1	0	2	0	1	1	1	1	1	0
Tremarctos ornatus	2	1	1	1	1	2	1	1	1	1	1	1	0	0	2	0	1	1	0	1	1	0
Ursus americanus	2	1	1	1	1	2	1	1	1	1	1	1	0	0	2	0	1	1	0	1	1	0
Ursus arctos	2	1	1	1	1	2	1	1	1	1	1	1	0	0	2	0	1	1	0	1	1	0
Ursus maritimus	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ursus thibetanus	2	1	1	1	1	2	1	1	1	1	1	1	0	0	2	0	1	1	0	1	1	0
Arctictis binturong	1	1	1	1	1	2	1	1	1	1	0	0	0	0	1	0	0	0	0	1	1	0
Cryptoprocta ferox	1	1	1	1	1	2	1	0	0	1	0	1	0	0	2	0	0	1	0	1	1	0
Genetta genetta	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Genetta maculata	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paguma larvata	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

[a] note that independent digit movements were not observed in any of the carnivores.

[b] 'other' digit/forepaw movement = objects held down between forepaws

[c] 'other' digit/forepaw movement = clawing/scratching

[d] 'other' digit/forepaw movement = items rolled between forepaws

Appendix 3. The phylogeny used in the comparative analyses presented in Chapters 2-4 from Bininda-Edmonds et al. (1999).