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Functional Tradeoffs in Specialization for Fighting versus Running

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Abstract

Both locomotion and fighting are critical to survival and reproductive fitness in many vertebrate species. Yet, characters that make an individual good at fighting may, in many cases, limit locomotor performance and vice versa. Here I describe tests of three functional tradeoffs in the limb muscles of two breeds of domestic dogs that have undergone intense artificial selection for running (Greyhound) or fighting performance (Pit Bull). We found that Greyhounds differ from Pit Bulls in having relatively less muscle mass distally in their limbs, weaker muscles in their forelimbs than their hindlimbs, and a much greater capacity for elastic storage in the in-series tendons of the extensor muscles of their ankle joints. These observations are consistent with the hypothesis that specialization for rapid or economical running can limit fighting performance and vice versa. Variation in body form among dog breeds has been suggested to be largely a consequence of selection on the ontogenetic variation present in individual wolf-like dogs (Wayne, 1986a,b). This, plus recent work on the genetics of the canid skeleton, raise the possibility that pit bulls are a breed that has evolved by the retention of juvenile shape (i.e., neoteny) and greyhounds may represent an acceleration of shape ontogeny. Finally, functional tradeoffs that prevent simultaneous evolution of optimal performance in both locomotor and fighting abilities appear to be widespread taxonomically and may have been particularly important in the evolution of hominid anatomy and physiology.

Key words: locomotion, male-male aggression, muscle, *Australopithecus*, *Homo*.

Introduction

Although fighting is a behavior that occurs relatively rarely, it is widespread among vertebrates. When it does occur, it is both physically demanding and of great significance to survival and reproductive fitness (Geist, 1971; Berzin, 1972; Hamilton 1979; Silverman and Dunbar, 1980; Clutton-Brock, 1982; Enquist and Leimar, 1990; Andersson, 1994; Wrangham and Peterson, 1996). The evolutionary basis of fighting has received considerable attention from biologists (Darwin, 1871; Lorenz, 1966; Geist, 1971; Hamilton 1979; Parker, 1983; Huntingford and Turner, 1987; Enquist and Leimar, 1990; Andersson, 1994), but the physiology and functional morphology of fighting remain largely unstudied. This lack of work on the mechanics and physical demands of fighting stems in large part from the intrinsic difficulties of measuring physiologically relevant variables in fighting subjects. Physiologists and morphologists may also have shied away from studying fighting because of ethical concerns associated with eliciting fighting behavior in a controlled, laboratory setting and because the violence of fighting is an unpleasant topic to think

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about and discuss. Nevertheless, I believe fighting has played a far greater role in the evolution of many vertebrate groups than is generally recognized. If this is true, and a major goal of evolutionary morphology is to understand the physiological basis of vertebrate diversity, then fighting is a behavior that warrants far greater attention from physiologists and morphologists than it has received in the past.

Here I consider functional tradeoffs entailed by the requirements of locomotion versus the requirements of fighting that may be particularly important in the evolution of vertebrate diversity. Both locomotion and fighting are critical to survival and reproductive fitness in most vertebrate species. Yet, characters that make an individual good at fighting may, in many cases, limit locomotor performance and vice versa (Hamilton, 1979; Pasi and Carrier, in press). For example, among apes, sexual dimorphism in body size and male-male fighting are most dramatic in gorillas (Nowak and Paradiso, 1983). Large body size allows dominant male gorillas to defend multifemale groups against lone males interested in attracting the females and killing the infants (Fossey, 1983; 1984; Watts, 1989). Large size, however, severely limits the ability of male gorillas to climb trees (Schaller, 1963). In contrast, both male and female gibbons brachiate with spectacular grace and agility. Gibbons exhibit little or no sexual dimorphism in body size and mate in monogamous pairs (Nowak and Paradiso, 1983; MacKinnon and MacKinnon, 1984). Both male and female gibbons participate in defense of territory and aggressive encounters rarely involve physical contact (Preuschoft et al., 1984; Mitani, 1987). This comparison illustrates what I believe is a general trend; locomotor performance is constrained in fighting specialists whereas fighting ability is limited in locomotor specialists. In the discussion that follows, I consider possible functional tradeoffs in the limb muscles of fighting versus running specialists, and the potential implications of these tradeoffs to the evolution of both hominids and fighting breeds of domestic dogs.

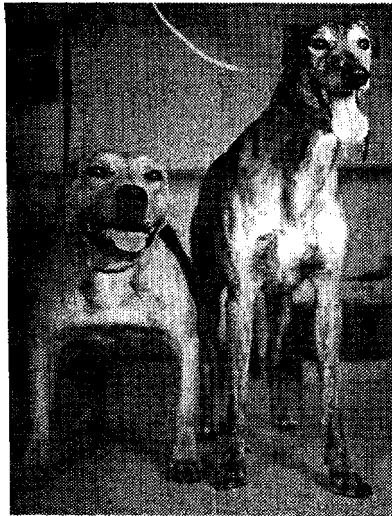


Figure 1. Frontal view of representatives of the two breeds of domestic dogs used to study specialization for running versus specialization for fighting: greyhounds and pit bulls. Both individuals in this photograph are adult males with a body mass of 33 kg. Modified from (Chase et al., 2002).

Specialization of limb muscles for fighting versus running

To test hypotheses of functional tradeoffs in muscle specialization for high speed and/or endurance running versus fighting performance, we have compared anatomical determinants of muscle function in two breeds of domestic dogs (Fig. 1, Pasi and Carrier, in press). Although there are well recognized limitations associated with two species (or breed) comparisons when studying adaptation (Garland & Adolph, 1994; Garland, 2002), the choice of greyhounds and pit bulls ameliorate the problems in substantial ways. First, the types of selection these two breeds have experienced are known and were very specific. Greyhounds are a breed that has experienced intense selection for maximum running speed and anaerobic (burst) stamina. In contrast, pit bulls are derived from several breeds specialized for fighting and, since their inception, they have undergone intense selection for physical combat with other dogs. In both cases, selection by the breeders appears to have driven the breeds to extreme specialization. Second, the environment in which the two breeds have evolved has been largely controlled. That is, both breeds have evolved as domesticated animals in which humans provided their day-to-day care and determined their survival and reproduction. Thus, although differences between the two breeds may exist due to genetic drift, adaptive differences other than those due to selection for fighting or running are unlikely to exist. In summary, the comparison of pit bulls and greyhounds represents an unreplicated selection experiment. But it is a selection experiment that has potential to falsify hypotheses of muscle specialization, and one that may provide additional insight to the nature of functional tradeoffs between running and fighting.

Proximal to distal distribution of limb muscle mass

Tetrapods that are specialized for fighting can be expected to have relatively larger muscles located distally in their limbs than is the case in tetrapods that are specialized for running. The mechanical work of locomotion can be divided into two components, the work required to accelerate and decelerate the mass of the animal during each step and the work required to swing the limbs relative to the center of mass of the animal. This latter component is referred to as the internal work of locomotion. At high running speed or in animals with heavy limbs, such as hominids, the internal work can constitute a significant portion of the total mechanical work of running (Cavagna and Kaneko, 1977; Fedak et al. 1982; Willems et al. 1995). This leads to the expectation that animals specialized for economical running will have relatively less muscle mass in their distal limbs to reduce the rotational inertia of the oscillating limbs (Hildebrand and Hurley, 1985; Steudel, 1991). In contrast, we expect the distal limbs of animals specialized for fighting to be well muscled to allow the production of large forces and high power for opponent manipulation. This distinction appears to hold among many species comparisons. Consider the comparison of apes given above, or the comparison of lions and cheetahs. The distinction also exists between pit bulls and greyhounds (Pasi and Carrier, in press). Pit bulls have a greater percentage of their limb muscle mass distal to the elbow and knee joints than do greyhounds (Fig. 2A). Hence, the relative robustness of distal limbs may help distinguish fighting from locomotor specialists.

Relative muscular strength of fore and hindlimbs

The contractile physiology of muscle leads us to expect that the relative strength of fore and hindlimb muscles will be different in runners and fighters (Pasi and Carrier, in press). Because active skeletal muscle generates much greater force when it is stretched (eccentric contraction) than when it shortens (Katz, 1939) we expect quadrupedal animals specialized for running to have less muscle strength in their forelimbs than in their hindlimbs. This hypothesis emerges from the observed division of labor in the limbs in which the forelimbs of running animals play a greater role

in deceleration and hindlimbs play a greater role in acceleration (Cruse, 1976; Cavagna et al., 1977; Jayes and Alexander, 1978; Heglund et al., 1982; Blickhan and Full, 1987; Full et al., 1991). Because the extensor muscles of the limbs must actively stretch to absorb energy during deceleration, but must actively shorten to produce acceleration, less muscle will be required in the forelimbs than the hindlimbs. In contrast, the extensor muscles of the forelimbs of animals specialized for fighting can be expected to be as large or larger than those of the hindlimbs because forelimbs are often used to maintain balance and to strike and manipulate an opponent during fighting.

Here also comparison of closely related species seems to support the expectation. The hindlimbs of cheetahs appear to have more muscle mass than the forelimbs, whereas the muscle mass of the forelimbs of lions appears to be greater than that of their hindlimbs. Similarly, our comparison of the relative strength (cross sectional area) of the extensor muscles in the forelimb and hindlimb of dogs shows that greyhounds have stronger extensor muscles in their hindlimbs than in their forelimbs, whereas the pattern is reversed in pit bulls, who have greater or equal strength in the extensor muscles in their forelimbs than in their hindlimbs (Fig. 2B; Pasi and Carrier, in press).

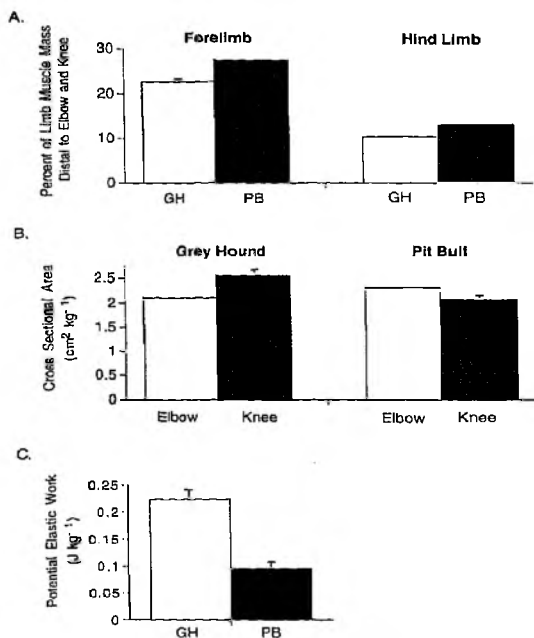


Figure 2. A) Percent of total limb muscle mass distal to the elbow and knee joints in four greyhounds and five pit bulls. In each comparison, the percent of muscle mass in the distal limb is significantly greater in the pit bulls. B) Comparison of the average cross sectional area of the extensor muscles of the elbow and knee joints in four greyhounds and five pit bulls. The greyhounds have stronger muscles in their hindlimbs, whereas the pit bulls have stronger muscles in their forelimbs. C) Comparison of the average potential for storage and recovery of elastic strain energy in the tendons of the extensor muscles of the ankle joint in four greyhounds and five pit bulls. These data are based on measurements of muscle and tendon cross sectional area, and tendon length. From Pasi and Carrier, in press.

Potential for storage and recovery of elastic strain energy

Tetrapods specialized for fighting are expected to have little or no capacity to store and recover elastic strain energy in the muscle tendon systems of their limbs. Elastic storage and recovery of strain energy in the tendons of distal limb muscles is thought to greatly enhance the economy of transport during both low and high speed running (Cavagna et al. 1964; Dawson and Taylor, 1973; Taylor, 1994; Alexander, 1984; Roberts et al. 1997; Biewener, 1998). For this reason we expect animals specialized for distance and/or high speed running to have a high capacity for elastic storage, i.e., long stretchy tendons. In contrast, long stretchy tendons in series with extensor muscles would likely be a handicap for any animal attempting to over-power an opponent during physical combat. Hence, we expect animals specialized for fighting to have relatively limited abilities to use elastic storage during running. Breeds of domestic dogs selected for running and fighting appear to fit these expectations. Our analysis of muscle and tendon metrics indicated that greyhounds have more than a two-fold greater capacity to store and recover elastic strain energy in the extensor muscles of their ankle than do pit bulls (Fig. 2C; Pasi and Carrier, in press).

Summary

We tested three hypotheses of functional tradeoff by measuring determinants of limb musculoskeletal function in two breeds of domestic dogs that have undergone intense artificial selection for running or fighting performance (Pasi and Carrier, in press). We found that pit bulls differ from greyhounds in having relatively greater muscle mass distally in their limbs, relatively stronger muscles in their forelimbs than their hindlimbs, and a much lower capacity for elastic storage in the extensor muscle-tendon systems of their ankle joints. These observations are consistent with the hypothesis that specialization for fighting performance can limit rapid or economical running and vice versa.

Are Pit Bulls neotenic wolves?

The anatomical differences between greyhounds and pit bulls (Fig. 1) are remarkable given that these differences exist in members of the same species. Wayne (1986a,b) has suggested that the great diversity of body form observed among breeds of domestic dogs is largely a result of heterochronic alteration of postnatal growth rates. His analysis of skeletal allometry has shown that for both limb and cranial dimensions the extent and direction of breed evolution appears to be reflected in the ontogeny of a single domestic dog. If the variation in body form among breeds is largely a consequence of selection on the ontogenetic variation present in individual wolf-like dogs, as Wayne suggests (1986a,b), then pit bulls are a breed that has evolved by the retention of juvenile shape (i.e., neoteny) and greyhounds may represent an acceleration of shape ontogeny.

Recently Chase et al., (2002) have identified three principle components of skeletal metrics in Portuguese water dogs that are highly heritable and associated with quantitative trait loci (QTLs). They suggest the QTLs are consistent with regulatory genes that control skeletal ontogeny in domestic dogs. In one principle component, metrics of pelvic size are inversely correlated with metrics of snout length. In another, metrics of the length of the skull and limbs are inversely correlated with metrics of skull width and height, including those that define cranial volume. The last principle component shows an inverse correlation between skull and limb lengths with widths of limb and axial skeletal elements. Thus, Chase et al., (2002) suggest that appropriate temporal activation of different genes associated with these three principle components could produce the short face and limbs as well as the stout pelvic girdles and limb bones of young puppies on the one hand, followed by development of the longer face and more gracile limbs of adult dogs on the

other. They also suggest these principle components could be the basis of much of the evolution of skeletal proportions in breeds as diverse as greyhounds and pit bulls.

These observations raise the possibility that retention of early juvenile characters (i.e., neoteny) may be a mechanism by which artificial selection has produced fighting specialization in domestic dogs such as pit bulls. This suggestion is bolstered by the apparent selective environment of newborn mammals of many species. The mammalian system of nursing physically dependent young requires a suite of motor skills in newborns that allow nursing and competition with siblings for access to mom's nipples. In newborn mammals, the relatively short muzzle (de Beer, 1985) is thought to facilitate suckling (Emerson and Bramble, 1993) and their relatively stout neck, trunk, and limbs likely help individuals defend access to nipples and displace competing siblings from nipples. Thus, a body configuration appropriate for certain types of physical combat may be a basal feature of neonatal placental mammals. If this were true, retention of neonatal characters in adults might provide a mechanism for rapid evolution of specialization for fighting.

Were early hominids specialized for fighting?

Stature and shape of *Australopithecus*

Much of what distinguishes the postcranial body of *Australopithecus* from that of *Homo* are plesiomorphic traits generally thought to be associated with an arboreal habitat in the case of *Australopithecus* (Stern and Susman, 1983) versus adaptations for improved distance transport in *Homo* (Wolpoff, 1999). Nevertheless, the anatomical traits that distinguish australopithecines from members of the genus *Homo* (Fig. 3) are in many cases parallel to those that distinguish pit bulls from greyhounds (Fig. 1).

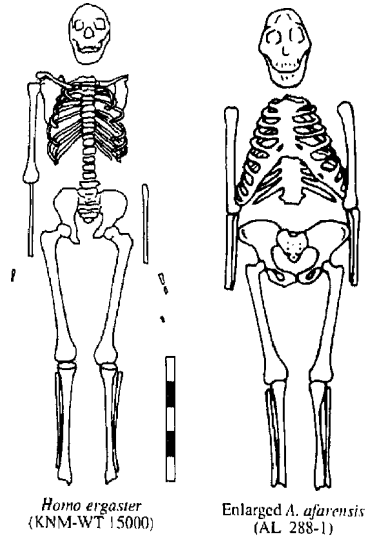


Figure 3. Illustrations of the skeletal anatomy of *Homo ergaster* and *Australopithecus afarensis*. The drawing of *A. afarensis* has been scaled up to the same height as *H. ergaster* to better illustrate the differences in proportions. Modified from Klein (1999).

Australopithecines had a short, broad stance, relatively powerfully forelimbs, and a robust head and neck similar to the configuration of pit bulls. In contrast, humans have longer legs, relatively narrower limb girdles, and more gracile forelimbs and body, similar to that of greyhounds. Based on this analogy with pit bulls and greyhounds, I suggest many traits that distinguish australopithecines from both their arboreal ancestors and from *Homo* are due, at least in part, to specialization for fighting in *Australopithecus* (Carrier, 2003).

Many of the characters that gave australopithecines a fighting physique, however, clearly represent a legacy inherited from arboreal ancestors. Indeed, a component of the fighting hypothesis, presented here, is that adaptations for climbing preadapted hominoids for fighting with the forelimbs in the manner of chimps, gorillas, and humans. Nevertheless, distinguishing between plesiomorphic arboreal characters that convey a performance advantage in fighting from traits that are associated with specialization for fighting is beyond the scope of this review, but is discussed in some detail elsewhere (Carrier, 2003).

Distribution of mass within the limbs

The distal segments of both the fore- and hindlimbs of australopithecines appear to have been more robust and massive relative to body size than those of *Homo* (Fig. 3). Mid-shaft diameters of the radius and ulna suggest that the forearms of australopithecines were often exceptionally robust (Hartwig-Scherer, 1993; McHenry, 1986). Evidence of relatively massive forearms, compared to *Homo*, also emerges from analysis of the articular surfaces of the elbow joint (McHenry, 1978; McHenry, 1992; McHenry and Berger, 1998). Forearms of australopithecines appear to have been very long relative to humeral length (reviewed by McHenry and Coffing, 2000). Similarly, australopithecines are known to have had relatively larger hands and feet (Stern and Susman, 1983) and larger peroneal muscles (Tuttle, 1981; Stern and Susman, 1983) than *Homo*. Furthermore, the structure of the metacarpals and wrist bones of australopithecines suggest that the muscles of the forearm associated with wrist and finger flexion were large (Stern and Susman, 1983).

Certainly a component of the massive distal limbs of australopithecines can be explained by specialization for climbing (Stern and Susman, 1983; Hunt, 1998), whereas the relative reduction in distal limb mass that characterizes *Homo* is consistent with improved locomotor economy (Hildebrand and Hurley, 1985; Steudel, 1991). Nevertheless, the exceptional sexual dimorphism in forelimb size and robustness observed among australopithecines (McHenry, 1991a; McHenry, 1996), discussed below, suggests that the massive distal limbs of australopithecines may also represent specialization for fighting (Carrier, 2003).

Forelimb versus hindlimb strength

One would expect hominids specialized for fighting to have had relatively strong forelimbs for opponent manipulation (Carrier, 2003). In contrast, those specialized for running can be expected to have had relatively weak forelimbs to reduce body mass, and strong hindlimbs to generate the needed locomotor forces and power. Compared to *Homo*, australopithecines had relatively less robust hindlimbs and significantly more massive forelimbs (McHenry, 1992; Fig. 3). Relative to their hindlimbs and sacral vertebrae both *A. afarensis* and *A. africanus* have robust forelimbs. This is particularly true of *A. africanus* which was similar in proportions to African apes (McHenry and Berger, 1998). In this case, as in the previous comparison of distal limb robustness, the difference between *Australopithecus* and *Homo* are likely to be due, at least in part, to climbing specialization in *Australopithecus* and specialization for terrestrial locomotion in *Homo*. But, here also, the dramatic sexual dimorphism in the size and robustness of the forelimbs of the australopithecines suggests

that the structure of their forelimbs may also have been influenced by selection for fighting performance (Carrier, 2003).

Elastic storage

Analysis of modern humans suggests that storage and recovery of elastic strain energy is an effective and important mechanism of energy conservation in human runners (Cavagna et al. 1964; Ker et al., 1987; Alexander, 1988). The potential of australopithecines to use elastic storage is difficult to access, but can be assumed to have been substantially less than that observed in modern humans (Bramble personal communication). It is known that the major sites of elastic strain are the in-series tendons, likely including aponeuroses, rather than the muscle tissue itself (Alexander, 1988). Furthermore, the amount of energy that can be stored in a tendon is a direct function of its length. Because tendon length is related to leg length, animals with relatively long legs tend to have longer tendons and a greater capacity for elastic storage than animals with relatively short legs. In our comparison of greyhounds and pit bulls, tendon length played the greatest role in determining the estimated two-fold difference in potential for elastic storage (Pasi and Carrier, in press). Hence, the short hindlimbs of australopithecines relative to larger bodied humans (Jungers, 1982; Wolpoff, 1983, 1999; Ruff, 1988; Fig. 3) lead to the suggestion that the potential for elastic storage was probably much lower in australopithecines than in modern humans (Carrier, 2003). As explained above, little or no potential to store and recover elastic strain energy in the muscle-tendon systems of the limbs would result in poor locomotor economy, but would likely improve fighting performance.

Sexual dimorphism in early hominids

Australopithecines appear to have had a higher level of sexual dimorphism in body size than is observed in *Homo*. Sexual dimorphism in australopithecines is apparent in their dentition (Wolpoff, 1976; Kimbel and White, 1988), limb bone lengths (McHenry, 1991b), limb bone robustness (Hartwig-Scherer, 1993; Lockwood et al., 1996), and limb joint size (McHenry 1991a, 1992). Based on an analysis of the mandibular corpus, proximal femur and humerus Lockwood and collaborators (1996) suggest that the level of body size sexual dimorphism in *A. afarensis* approached, but did not exceed that of the most dimorphic modern hominoids: gorillas and orangutans. An analysis of the robustness of both fore and hindlimb bones by Hartwig-Scherer (1993) suggests that the ratio of male to female body weight of *A. afarensis* was greater than that of any modern hominoid. Using measurements of the size of hindlimb joints, McHenry (1991a) found that *A. afarensis* had a moderate level of body size sexual dimorphism that was well above that seen in modern humans, somewhat greater than that of the two extant species of chimpanzee, and below the sexual dimorphism of gorilla and orang-utan. The extensive analysis of body weight dimorphism in early hominids by McHenry (1978, 1986, 1991a,b, 1992, 1994, 1996) leads to the conclusion that dimorphism declines through time from *A. afarensis* to *A. africanus* to *A. robustus* with a dramatic reduction in *H. erectus* (McHenry, 1996).

A high level of body size sexual dimorphism may be a basal characteristic of the great ape/hominid clade (Begun et al., 1997). *Oreopithecus bambolii* is a large bodied, late Miocene (8.5 - 9.0 Ma.) member of the great ape/hominid clade (Harrison, 1987; Sarmineto, 1987), and is represented by a relatively extensive fossil record (Harrison, 1991). Based on the dentition, as well as the cranial and postcranial material, Harrison (1991) estimates that the body mass of males ranged from 30-40 kg, whereas females were ranged from 15-20 kg. Thus, a level of body size sexual dimorphism that exceeds that of *Homo* may be basal for our group of primates.

The forelimbs of australopithecines appear to have been more dimorphic than the jaws, teeth, or hindlimbs (McHenry, 1996). In *A. afarensis*, for example, the difference between large and small

ulnae, radii, and capitates is as great or greater than that between males and females means of the most dimorphic apes (McHenry, 1986; 1991a; 1996). Forelimbs also appear to have been relatively dimorphic in both *A. africanus* and *A. boisei* as well (McHenry, 1996). Forelimb robustness in both genders of australopithecines might be argued to be consistent with selection for arboreal behavior. But, selection for climbing performance probably cannot explain the greater sexual dimorphism in forelimb robustness than hindlimb and spine robustness (Carrier, 2003). Certainly climbing cannot account for the sexual dimorphism in forelimb robustness in gorillas.

Analysis of extant taxa suggests that the sexual dimorphism in body and forelimb size in australopithecines was a product of selection for male-male aggression (Carrier, 2003). Although the belief that competing males rarely injure each other remains strongly held by many biologists (Lorenz, 1966; Barnett, 1967; Tinbergen, 1963), male-male aggression that results in injury or death is common among both vertebrates and invertebrates (Geist, 1971; Berzin, 1972; Hamilton 1979; Silverman and Dunbar, 1980; Clutton-Brock, 1982; Enquist and Leimar, 1990; Andersson, 1994; Wrangham and Peterson, 1996). When males compete physically, the potential for serious injury needs to be real for a male to achieve dominance (Darwin, 1871; Geist, 1971; Parker, 1983; Andersson, 1994). Hence it should not come as a surprise that the relative size of male weapons is strongly correlated with both the extent to which males are larger in body size than females and with the level of polygyny (Clutton-Brock et al, 1977; Hamilton 1979; Clutton-Brock et al., 1980; Parker, 1983; Jarman, 1983; Andersson, 1994). Kangaroos and gorillas represent particularly relevant examples. Kangaroos use their forelimbs as weapons in fighting. Among species of kangaroos, dimorphism in the mass of the forelimb musculature and length of the forelimbs is most pronounced in polygynous species (Jarman, 1983). Similarly, gorillas fight with their forelimbs (Wrangham and Peterson, 1996). Zihlman and McFarland (2000) found that the greatest sexual differences in lowland gorillas is in the weight of the forelimbs, weight of the forelimb trunk binding muscles, and in the epaxial muscles. Thus, given that the extant apes most closely related to australopithecines, *Homo*, *Pan*, and *Gorilla*, all use their forelimbs as weapons during male-male aggression (Wrangham and Peterson, 1996) we can be relatively confident that australopithecines did as well. These observations suggest that the high levels of sexual dimorphism in body and arm size in australopithecines were associated with selection for improved performance in male-male aggression (Carrier, 2003).

Relationship between vertical climbing, bipedal posture, and fighting with forelimbs

Specialization for vertical climbing and forelimb suspension preadapts a lineage for fighting with the forelimbs, both because it predisposes an organism to bipedal posture and because it results in long and powerful forelimbs with high mobility (Carrier, 2003). The ancestor of modern hominoids is thought to have been an arboreal catarrhine adapted for vertical climbing and forelimb suspension (Harrison, 1991; Rose, 1997; Ward, 1997; Begun et al., 1997). The outgroup to extant hominoids for which postcranial anatomy is best known, *Oreopithecus*, had a suite of characters that suggest it was an adept vertical climber that relied on forelimb suspension (Harrison, 1991). These include features that 1) strongly differentiated usage of the hind and forelimbs (i.e., long and robust forelimbs relative to hindlimbs), 2) increased ability to raise the forelimbs above the head, 3) gave greater potential for circumduction at the shoulder and pronation-supination at the elbow and wrist, 4) increased potential for powerful grasping of large diameter vertical supports with the hands, 5) allowed adoption of a more orthograde trunk posture, 6) increased potential for full extension of the hip and knee joints, 7) allowed greater ranges of rotation at the hip and knee joints and inversion-eversion at the ankle joint, and 8) increased potential for body weight to be supported by a single hindlimb. Although these eight abilities, present in extant great apes (Gregory, 1916, 1928; Morton, 1926; Hunt, 1991) and inferred from the postcranial anatomy of

Miocene hominoids (Harrison, 1991; Rose, 1997; Ward, 1997; Begun et al., 1997), are associated with selection for climbing and forearm suspension, each ability can be argued to enhance fighting performance. Highly mobile, long and robust forelimbs and hands would increase the potential for striking, grasping, and manipulating opponents with the forelimbs. An increase in orthograde trunk posture (5) and an increased ability to support the body bipedally on the hindlimbs (6, 7, and 8) would free the forelimbs to be used as weapons. Finally, associated with the arboreal behaviors of vertical climbing and forelimb suspension are powerful shoulder and brachial muscles that produce hoisting and lateral transfer of the body (Tuttle and Basmajian, 1974; 1978; Tuttle et al., 1983). These are the same muscles that can be inferred to be employed in arching, over-the-head and roundhouse punches that chimpanzees and gorillas are observed to use when fighting (Goodall, 1986; Wrangham and Peterson, 1996). Thus, selection for improved vertical climbing and forelimb suspension can be argued to preadapt a species for fighting with its forelimbs (Carrier, 2003).

Many quadrupedal mammals adopt a bipedal posture when fighting, such as rats, mice, squirrels, dogs, bears, tigers, and horses. Among apes, both chimpanzees and gorillas adopt a bipedal posture for threat displays (Jablonski and Chaplin, 1993), beating an opponent with the forelimbs (Livingstone, 1962; Goodall, 1986; Wrangham and Peterson, 1996), jumping on an opponent that is lying on the ground (Goodall, 1986), and grabbing an opponent to deliver bites (Goodall, 1986; Wrangham and Peterson, 1996). Chimpanzees also stand bipedally to use weapons such as rocks and clubs (Kortlandt, 1980; Goodall, 1986; de Waal, 1989; Wrangham and Peterson, 1996). Thus, bipedal posture allows the forelimbs to be used as weapons to beat, restrain, and manipulate opponents. For a species that is normally quadrupedal, adoption of an upright bipedal posture also significantly reduces rotational inertia of the body (Carrier et al., 2001; Lee et al., 2001), increasing the speed at which the individual can rotate to face a new direction, as well as increasing the speed and power with which a round-house blow can be applied to an opponent. Hence, characters that improve balance and strength in a bipedal stance would likely enhance fighting ability in a lineage of quadrupeds that uses forelimbs as weapons. These arguments lead one to the suggestion that the bipedal posture and locomotion of early australopithecines may have improved their fighting performance (Carrier, 2003).

In addition to using bipedal posture when fighting, male chimpanzees and bonobos appear to prefer to fight while on the ground rather than from an arboreal perch. The most violent and serious fights in both chimpanzees and bonobos occur on the ground (Goodall, 1986; Wrangham and Peterson, 1996; de Waal, 1986, 1989; Kano, 1992). In contrast, when attempting to avoid physical aggression from other males, both chimpanzees and bonobos retreat by climbing into trees (Goodall, 1986; deWaal, 1989; Kano, 1992). These observations highlight the importance of the terrestrial substrate during fighting in our closest living relatives and are consistent with the hypothesis that specializations for rapid terrestrial movement, and balance and strength in bipedal posture may improve fighting ability in hominoids. Thus, selection for increased male-male aggression may have helped draw the ancestors of australopithecines to the ground. Alternatively, the necessity of greater terrestrial specialization, due to the opening of their forested habitat, may have opened the door for greater fighting specialization in early australopithecines by freeing the forelimbs from their primary role in climbing. In either case, it is likely that as a consequence of terrestrial specializations early australopithecines had greater fighting abilities and were, therefore, more dangerous opponents than was the case in their arboreal ancestors (Carrier, 2003).

Summary

I am suggesting that australopithecines were specialized for male-male aggression (Carrier, 2003). First, many aspects of the australopithecine musculoskeletal system, such as long powerful forelimbs, limited potential for storage and recovery of elastic strain energy in muscle-tendon

systems, and a propensity for orthograde, bipedal posture appear to have conferred high potential for fighting. Although most or all of these features were characters inherited from arboreal ancestors, they would have conferred high fighting performance in the first hominids. Second, the greater sexual dimorphism in body and forelimb size in early australopithecines relative to *Homo* is consistent with greater levels of male-male aggression, at least in the sense of simple arm-to-arm combat. Third, it can be argued that specialization for terrestrial locomotion and bipedal posture likely improve fighting performance in the hominoids from which australopithecines evolved. Thus, australopithecines appear to have been apes that were specialized for both a terrestrial locomotion and for male-male aggression.

Implications to the evolution of *Homo*

A false dichotomy?

Among the most conspicuous changes that occurred in the evolution of *Homo* from an australopithecine ancestor are an increase in body size, a reduction in relative forelimb length and robustness, a lengthening of the hindlimb, a reduction in the relative size of the feet, a relative narrowing of the pelvis, development of a more barrel-shaped chest, reduction in relative head mass, reduction of relative gut size, larger surface to volume ratio, and a drop in sexual dimorphism. Each of these changes can be argued to represent anatomical changes that would have facilitated economical transport and locomotor stamina (see above discussion and Carrier, 1984; Bramble, 1990, 2000; Jungers, 1991; Ruff, 1991, 1994; McHenry, 1994; Wolpoff, 1999). Within the context of the locomotor-fighting dichotomy, however, they are also changes in body configuration (excluding the increase in body mass) that would reduce male fighting ability (Carrier, 2003). If modern *Homo sapiens* are representative of the genus, however, male-male aggression and propensity for male violence are unlikely to have abated with the emergence of *Homo* (Wrangham and Peterson, 1996; Keeley, 1996; LeBlanc, 1999). Thus, our species is specialized both for locomotor stamina and male-male aggression. This appears to be in conflict with the suggestion that there are functional tradeoffs between selection for fighting specialization and selection for running specialization. Are the suggested functional tradeoffs between running and fighting a false dichotomy?

Cervids and bovids

Humans are not the only species that are both locomotor and fighting specialists. In terms of running speed and stamina three families of artiodactyls appear to be the top performers. Although cheetahs are often recognized as being the fastest runners on the planet, species in the artiodactyls families Cervidae, Bovidae, and Antilocapridae run almost as fast, and are known to have much greater stamina than the fastest cat (Nowak and Paradiso, 1983; Lindstedt et al., 1991). Yet these three families of artiodactyls are also recognized for their polygynous mating systems with intense male competition and male-male aggression (Geist, 1971; Jarman, 1989; Andersson, 1994). At first glance, these artiodactyls would appear to falsify the hypothesis of a running-fighting dichotomy. The basal weapons of mammals are teeth, claws, and limbs. But, cervids, bovids, and antilocaprids evolved teeth that are grinding machines for tough, fibrous plant material, and evolved limbs that function primarily as pogo sticks for economical transport. Thus, their basal weapons have become so specialized for feeding and locomotion that they no longer function as effective weapons. Each of these groups, however, evolved horns or antlers (Janus, 1982); new weapons that are largely independent of locomotion and feeding. By reducing conflicts with specialization for fighting, the evolution of these new weapons likely made extreme specialization of teeth and limbs possible in Cervidae, Bovidae, and Antilocapridae.

Invention of new weapon technology and the evolution of Homo

Analogous to the evolution of new weapons in bovids, cervids, and antilocapra, the invention of weapon technology by early hominids may have reduced the conflict between selection for locomotor stamina versus selection for male-male aggression, and allowed a greater independence in the evolution of characters associated with running and fighting (Carrier, 2003). In other words, the invention of new weapons may have allowed the evolution of locomotor specialization in the human lineage. Among cursorial mammals, modern humans are one of the best distance runners (Carrier, 1984). Humans are not fast runners, but we do have an ability to cover great distances more rapidly than most species. This ability is remarkable given our relatively recent arboreal ancestors and the relatively high energetic cost of human running. The physiological mechanisms that allow humans to be elite distance runners, in spite of their high cost of transport, are not well understood. Humans have been suggested to have 1) superior abilities to dissipate metabolic heat (Carrier, 1984; Wheeler, 1984, 1991; Porter, 1993), and 2) an ability to uncouple locomotor, ventilatory, and thermoregulatory functions that facilitates sustained vigorous running (Carrier, 1984). Recent work in sheep and dogs indicates that in species that pant to thermoregulate, and couple their ventilation to the locomotor cycle, regulation of body temperature during running does compete with both the minimization of ventilatory work and pH balance (Entin et al., 1998, 1999; Wagner et al., 1997). Thus, our relative independence of locomotor and ventilatory cycles, as well as cutaneous evaporative cooling, may give humans an advantage in endurance running relative to many other species. In any case, humans are elite endurance runners and hominids evolved this capacity in a relatively short period of time from ancestors that were not specialized for running. Anatomical features indicating cursorial specialization of *Homo*, mentioned above, appeared in the fossil record approximately 2.0 to 1.8 my ago (Klein, 1999; Wolpoff, 1999). The earliest stone tools appeared much earlier in the record at just over 2.5 my ago (Harris and Capaldo, 1993). Foley (1987) has argued on the basis of tool use by chimpanzees (Goodall, 1970; Boesch and Boesch, 1983), that simple tool use is an ancestral hominid trait that may have had its origin in the Miocene hominoids. Use of weapons, a category of tool, also likely predate the origin of hominids. Although the primary weapons of chimpanzees are their forelimbs and teeth, they also occasionally attack by throwing rocks (Kortlandt, 1980; Goodall, 1986; de Waal, 1989) and wielding branches as clubs (Kortlandt, 1980). Thus, we can be relatively confident that early australopithecines used simple weapons.

Summary

The observation that modern humans are both elite distance runners and a physically violent species appears to defy the hypothesis of functional tradeoffs between specialization for locomotion and specialization for fighting. Humans as well as bovids, cervids, and antilocapra, however, may be the exceptions that prove the running-fighting dichotomy. All three groups appear to have evolved exceptional locomotor performance in association with the evolution or invention of new weapon systems that are largely independent of locomotion (Carrier, 2003). Thus, the evolution of *Homo* may have been dependent on the invention of weapons that allowed specialization for locomotion and fighting to proceed independently.

Conclusions

In this discussion, I have presented three arguments to highlight the likely importance of selection for improved fighting ability in the evolution of vertebrate lineages. First, the physical demands of running and fighting entail functional conflicts that limit simultaneous evolution of improved performance in fighting and increased economy and speed in running (Pasi and Carrier, in press).

Second, these functional tradeoffs may be reflected in the postnatal ontogeny of many species of mammal, in which the demands of sibling competition require fighting specialization in neonates, but the demands of making a living and survival require running specialization in adults (Chase et al., 2002). This raises the possibility that retention of early juvenile characters (i.e., neoteny) may be a mechanism by which selection can produce fighting specialization in adults. Third, Hominidae appears to illustrate the degree to which a lineage can be influenced by selection for improved fighting ability. I have suggested 1) that selection associated with male-male aggression was instrumental in the evolutionary origin of the first hominids and 2) subsequent invention of new weapon technology allowed cursorial specialization in *Homo* (Carrier, 2003).

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