

Causes of sexual dimorphism in performance traits: a comparative approach

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ABSTRACT

Questions: Are there differences in whole-animal performance between the sexes, and what are the causes of this sexual dimorphism?

Organisms: Humans, horses, greyhound dogs, pigeons, and lizards.

Methods: We analysed performance records of human athletes, racehorses, greyhound dogs, racing pigeons, and lizards with respect to sexual dimorphism. Using the lizard data set, we correlated sexual dimorphism in running performance with sexual size dimorphism, reproductive effort, and territoriality.

Results: The athletic abilities of male organisms are generally greater than those of females. The difference is much more pronounced in humans than in horses, greyhound dogs, and pigeons. Within lizards, males are generally faster than females, but do not differ consistently in endurance. Among lizard species, body size dimorphism, territoriality, and reproductive effort do not predict the degree of sexual dimorphism in performance.

Keywords: fecundity, natural selection, sexual selection, territoriality, whole-animal performance.

INTRODUCTION

On 25 June 2005, the Jamaican athlete Asafa Powell set a new men's world record of 9.77 s over 100 m. If Florence Griffith Joyner, the then women's world record holder at 10.49 s, had competed in that race, she would have finished 10th and last. Why do male athletes tend to outrun female contestants? How general is this male supremacy in physical performance? Does sexual dimorphism in performance vary with the type of activity considered? Does it differ among species? And what are the proximate and evolutionary causes of this dimorphism?

While biologists have studied the possible origin of sexual dimorphism in body size, shape, and colour for over 150 years, they have rarely explored the causes of inter-sexual differences in whole-animal performance (Lailvaux *et al.*, 2003). This is surprising, because the

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study of ecologically relevant whole-animal performance is central to our understanding of how morphological (and other) traits affect fitness (Bartholomew, 1966; Arnold, 1983; Kingsolver and Huey, 2003). Examining the causes and consequences of sexual dimorphism in performance may yield important insights into the mechanisms and targets of natural and sexual selection. We here combine disparate types of data to illustrate that sexual dimorphism in performance is both as real and as variable as dimorphism in morphology, and that its evolutionary origins remain obscure.

VARIATION IN SEXUAL DIMORPHISM IN PERFORMANCE

Among-functions variation in human performance

Figure 1 depicts the degree of sexual dimorphism in a variety of sporting competitions that allow direct comparison of male and female performance. Results for several other disciplines (e.g. shot put, discus throw, javelin throw) were not considered, because different rules apply for male and female contestants (e.g. weight of the discus). We used the world records (as listed on 1 June 2007 by the respective international organizations) for adult men and women to calculate the two-step ratio index of sexual dimorphism. This index, coined by Lovich and Gibbons (1992) and modified by Smith (1999), defines sexual dimorphism as:

- (male trait value/female trait value) if the male value exceeds the female value
- $2 - (\text{female trait value}/\text{male trait value})$ if the female value exceeds the male value

Over the 50 field-and-track, rowing, swimming, and speed skating events considered, the mean sexual dimorphism in performance amounted to 1.11 (standard deviation = 0.03). In all cases, the men's world record was sharper than that of the women. Sexual dimorphism was lowest for lightweight single scull rowing (1.07) and highest for the pole vault (1.23). Comparison of performance in the weight lifting events was more cumbersome, because athletes compete in different classes according to their body mass (men: <56, <62, <69, <77, <85, <94, <105, and 105+ kg; women: <48, <53, <58, <63, <69, <75, and 75+ kg). We therefore fitted a quadratic regression to the women's body mass–performance data for each of the three competitions (clean-and-jerk, snatch, and combined). We used these equations to predict the women's performance at a body mass corresponding to each of the men's body mass classes. For the open classes, we used the body masses of the current world record holders. We then calculated sexual dimorphism at a particular body mass using the actual male and virtual female performance data. Thus computed, sexual dimorphism in weight lifting performance is the highest of all sporting competitions considered (between 1.26 and 1.40, mean = 1.34).

Sports sociologists pointed out long ago that comparing current world record performances between men and women may be equivocal because (1) official women's competitions began later than those of the men, and (2) even today, socio-cultural conditions are such that fewer women than men participate in competitions (Eagly, 1987; Eagly and Wood, 1999). It has been argued that, because of these factors, women's competitions have yet to reach the level of those of the men, but that, given time, women will eventually catch up with men (Tatem *et al.*, 2004). As a limited test of this idea, we used data on the progression of world records through time to estimate 'ultimate' records for men and women. The analysis of record data and the prediction of future sporting results have a rich tradition (for a limited

review, see Terpstra and Schauer, 2007). We here use a simple asymptotic regression model (Chatterjee and Chatterjee, 1982; see also Morton, 1984; Chatterjee and Laudato, 1997; Liu and Schutz, 1998; Kuper and Sterken, 2003). The regression model is

$$y = a + b \exp(cx)$$

where a , b , and c are constants and y is the record at time x . The parameter a is the asymptotic value of $y(x)$ and can be used as an estimate of the ‘ultimate’ world record. We used the LAB Fit software (Silva and Silva, 2007) to fit the regressions. We visually inspected each fitted line. For multiple reasons (e.g. change of competition rules, technical developments), the progression curves for several records showed obvious deviations from a smoothly inclining or declining curvilinear path. In these cases, we deleted the data preceding the abnormality. We refrained from predicting asymptotic values for those sporting competitions for which there was no indication of a decline in the rate of performance improvement. We obtained seemingly reliable output for 30 sporting competitions. Sexual dimorphism in ‘ultimate’ performance was calculated using the asymptotic values for men and women.

The procedure yielded an estimated mean sexual dimorphism in performance of 1.11 (standard deviation = 0.060, range: 1.00–1.21), suggesting no further systematic change in the difference between men’s and women’s performance in the future (paired t -test between current and ‘ultimate’ world records, $t_{29} = 0.14$, $P = 0.98$). Our result is in line with recent conclusions that the difference in athletic performance between the sexes has stopped being reduced (Sparling *et al.*, 1998; Chevront *et al.*, 2005; Seiler *et al.*, 2007). This suggests that the differences in performance between the sexes reflect true ‘biological’ differences between males and females and do not merely reflect women’s lesser participation in sport, or inferior training practice (Seiler *et al.*, 2007).

Several authors have argued that for morphological and physiological reasons, men will dominate sports that depend on strength and anaerobic capacity, whereas women will perform better at ultralong-distance aerobic events (Wells, 1991; Chatterjee and Laudato, 1997; Coast *et al.*, 2004; Beneke *et al.*, 2005). Examination of the sexual dimorphism in world records for running across a wide range of distances lends little support to this idea (Fig. 2). Coast *et al.* (2004) compared the relative running performances of men and women over distances between 100 m and 200 km and found the difference between the sexes to increase with distance, rather than to decline. The interpretation of these results may be clouded, however, by the proportionately under-representation of women in runs of longer distance (Coast *et al.*, 2004). Similarly, there is no clear evidence for an effect of distance on sexual dimorphism in speed skating performance (Fig. 2). Gender differences in free style swimming world records do seem to shrink with increasing distance (Fig. 2) (see also Tanaka and Seals, 1997). Why an effect of distance on sexual dimorphism in performance should be apparent in swimming but not in running is unclear. It may be linked to the fact that locomotor economy is similar for men and women on land (Pate *et al.*, 1987; Daniels and Daniels 1992), but not in the water (Pendergast *et al.*, 1977; Lavoie and Montpetit, 1986). It is possible that the lower locomotory cost to women in the water becomes more important at longer distances (Tanaka and Seals, 1997).

Among-species variation in locomotor performance

Is male supremacy in athletic performance idiosyncratic for the human species, or do other animals show a similar pattern? With a few exceptions (see below), comparisons of the

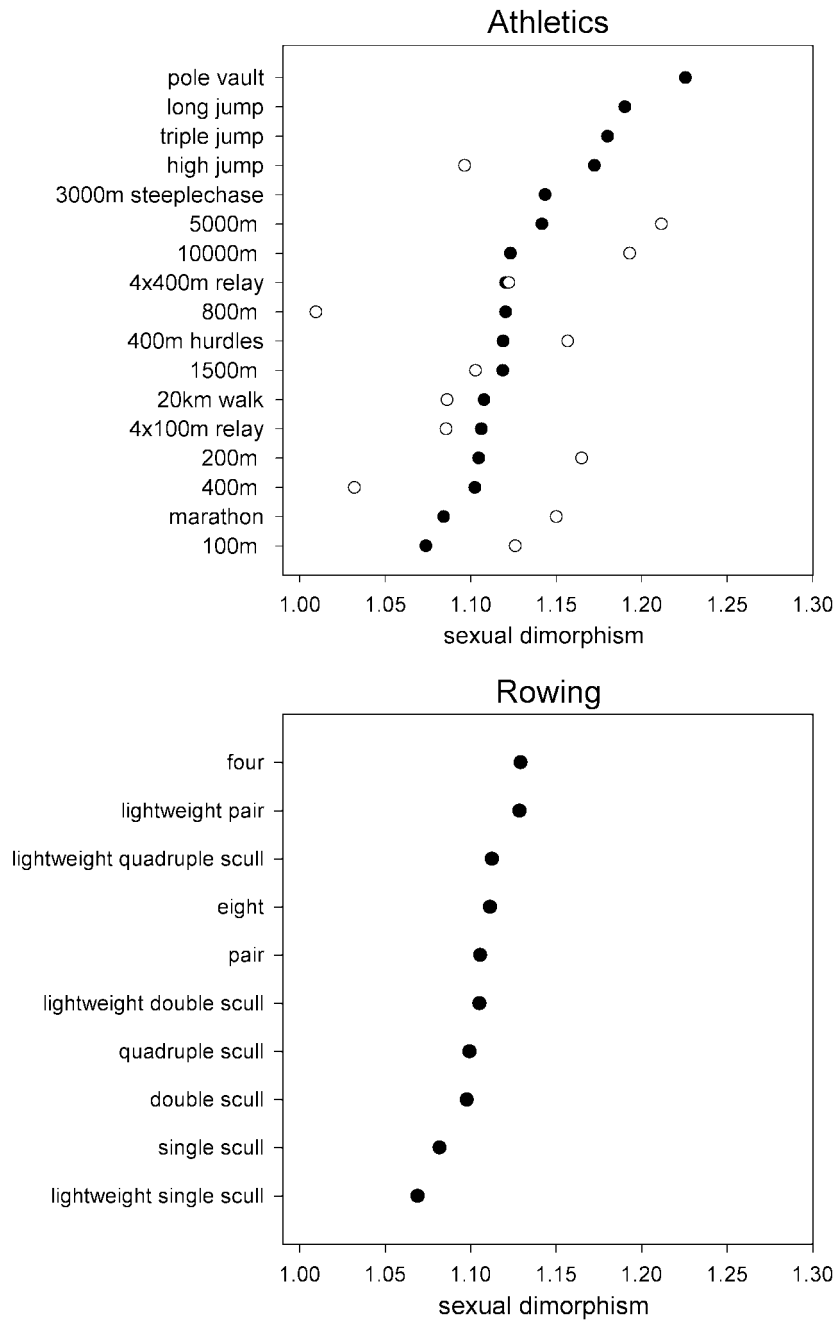
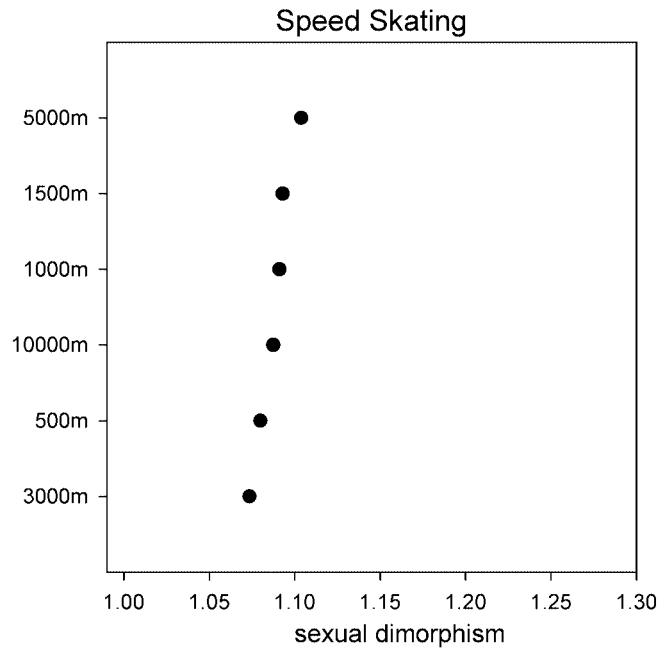
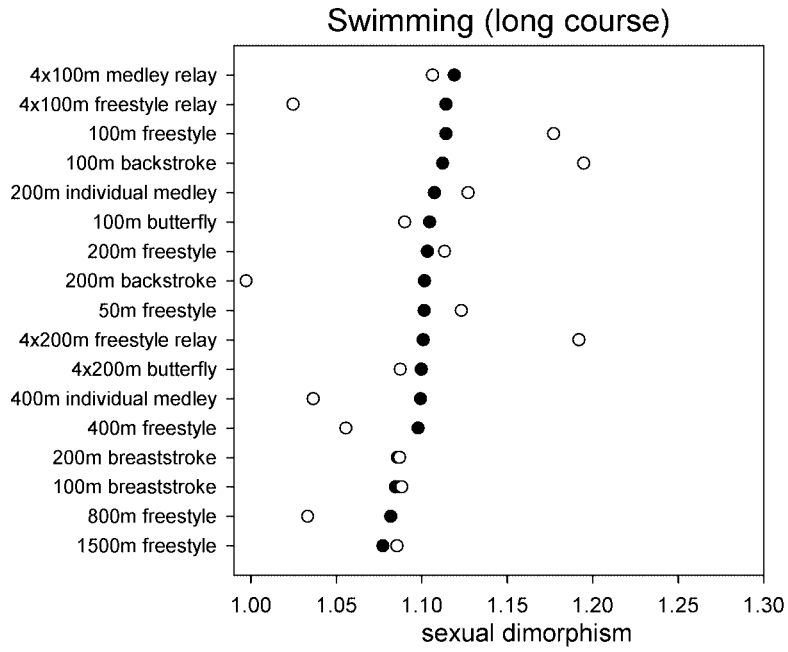


Fig. 1. Sexual dimorphism in human athletic performance in various sports: athletics, long course swimming, rowing, and speed skating. Solid symbols indicate sexual dimorphism calculated from



current (10 July 2007) world records; open symbols indicate sexual dimorphism in projected ('ultimate') world records (see text for details).

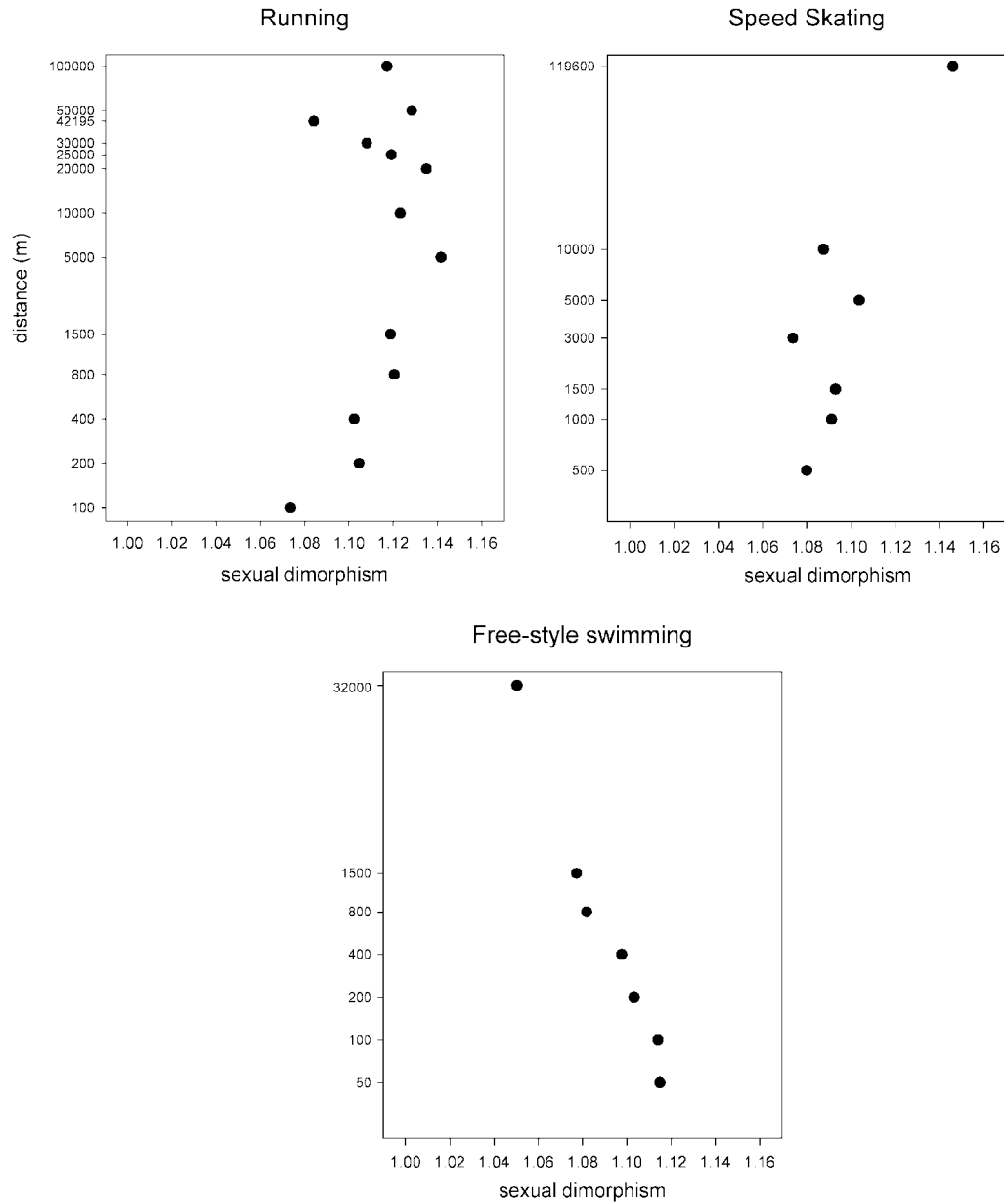


Fig. 2. Sexual dimorphism in human running, speed skating, and free-style swimming records, as a function of distance. In addition to the data for the traditional ‘Olympic’ distances, we show those for 20, 25, 30, 50, and 100 km running, the Dutch ‘Elfstedentocht’ (a speed skating race over close to 120 km), and English Channel crossings.

performance capacity of male and female animals from natural populations are rare (Lailvaux *et al.*, 2003). However, for a number of vertebrate species that are used in racing sports, sex-specific performance records are readily available. We will briefly review the

sexual dimorphism in locomotor performance of horses, greyhound dogs, and racing pigeons. Please note that these three groups of animals have been subject to unusually strong selection for speed for many years, which may hinder extrapolation of our findings to natural populations.

P. Entin (in preparation) has analysed results from thoroughbred horse races on tracks in the USA, France, and Australia, comparing average velocities of intact and neutered winning males and females over two distances (≤ 1609 m, > 1609 m). Although on average intact males were significantly faster than females and geldings, the sexual dimorphism was only 1.007 in the shorter races and 1.014 in the longer races. Similarly, for standard-bred horse races from American tracks (all 1609 m), the sexual dimorphism amounted to a humble 1.015 for trotters and less than 1.001 for pacers.

For greyhounds, we analysed the running times of male and female dogs competing in races on eight Irish tracks between 2001 and 2005. Running distances ranged between 274 and 759 m. We calculated sexual dimorphism in running performance for a total of 106 races, involving 1488 bitches and 3962 male dogs. The mean sexual dimorphism was 1.00026 (standard deviation = 0.0026).

We also compared the mean speeds of male and female racing pigeons returning from distances between 126 and 622 km to their home loft in southern England. We calculated the sexual dimorphism in flying performance for 16 different races, using the average speed of the five best cocks and hens per race. We found a mean sexual dimorphism of 1.023 (standard deviation = 0.034). There was no indication that sexual dimorphism was dependent on the distance covered.

Even when considering the data from this small set of vertebrates, it becomes apparent that sexual dimorphism in performance varies considerably among species. Below, we review possible proximate and ultimate reasons for the dimorphism, and for its variability.

PROXIMATE ORIGINS OF SEXUAL DIMORPHISM IN PERFORMANCE

Many medical and sports sciences studies have reported differences between the sexes in morphological, physiological, and endocrinological variables that are likely to affect human athletic ability. One of the most obvious variables is body size. Although sexual size dimorphism varies somewhat among human populations (Gustafsson and Lindenfors, 2004), mean stature in males is invariably greater than in females (Eveleth, 1975). The mean sexual size dimorphism is approximately 1.07 (Gaulin and Boster, 1985; Gustafsson and Lindenfors, 2004). Body size can exert its effect on performance in multiple ways. For instance, under isometric scaling, larger bodies would imply longer limbs, which may extend stride length by providing greater forward propulsion (Jones and Lindstedt, 1993; Van Ingen Schenau *et al.*, 1994). Stride length is the prime kinematic determinant of top speed in humans (Weyand *et al.* 2000), and many other vertebrates (e.g. Alexander, 1989; Vanhooydonck *et al.*, 2002). Because they have larger body masses, male humans on average also have larger absolute muscle masses (e.g. Janssen, 2000) and therefore can exert more power during physical exercise than females (e.g. Weber *et al.*, 2006). Larger bodies typically also accommodate larger lung volumes and diffusion surfaces (McDonnell and Seal, 1991) and larger hearts (e.g. Wiebe *et al.*, 1998; Wernstedt *et al.*, 2002), providing males with better pulmonary (Harms, 2006) and cardiovascular (Charkoudian and Joyner, 2004) function. These differences likely account at least in part for the observed sexual dimorphism in maximum oxygen consumption ($\dot{V}O_{2\max}$) (Åstrand and Rodahl, 1974; Wernstedt *et al.*, 2002; Harms, 2006), long considered the key physiological index of aerobic performance capacity.

In addition, men and women differ in many morphological and physiological features likely to affect physical performance, even after removal of the effect of body size differences. For a given body size, women tend to have less muscle mass and more fat mass (Sparling and Cureton, 1983; Ley *et al.*, 1992). In addition, women typically have a lower proportion of their lean tissue distributed in the upper body, which may be responsible for the difference in upper body strength between the sexes (Miller *et al.*, 1993). Differences in the amount and distribution of body fat produce differences in buoyancy characteristics between the sexes, probably offering female swimmers an advantage over their male counterparts in using natural buoyancy to improve swimming performance (McLean and Hinrichs, 2000). The mean cross-sectional area of muscle fibres is substantially higher in men than in women (e.g. Miller *et al.*, 1993; Staron *et al.*, 2000). Also, although there seems to be no systematic difference in overall fibre type distribution between the sexes, women tend to have a higher percentage of slow-twitch muscle fibres, whereas men have a higher percentage of fast-twitch IIA muscle fibres (Essén-Gustavsson and Borges, 1986; Staron *et al.*, 2000). Differences in these characteristics of the muscle likely contribute to differences in athletic performance (Gollnick and Matoba, 1984). Several traits of the cardiovascular and respiratory systems also exhibit sexual dimorphism, even when differences due to body size are accounted for. Women on average have smaller blood volumes, lower circulating haemoglobin concentrations, and hence lower oxygen-carrying capacity than men of comparable body size (Charkoudian and Joyner, 2004). These factors contribute to the smaller $\dot{V}O_{2\max}$ measured in women, even when accounting for differences in lean body mass. It is likely they also play an important role in the lower average performance of women in endurance exercise performance (Joyner, 1993). Although the increase of stroke volume during exercise is similar in men and women, women begin with relatively smaller resting stroke volumes than men, and end up with lower maximal cardiac output and $\dot{V}O_{2\max}$ (Wiebe *et al.*, 1998). Lung morphology is also sexually dimorph, with men having larger diameter airways (Mead, 1980) and larger lung volumes (Crapo *et al.*, 1982) and diffusion surfaces (Thurlbeck, 1982; Schwartz *et al.*, 1988) than size-matched women. These structural differences may make women more susceptible to pulmonary limitations during exercise than men (Harms, 2006). In general, the above-mentioned structural and functional differences imply that men are better equipped than females to compete in sports that require strength, speed, and endurance. There is also evidence that men and women differ in the relative utilization of carbohydrates and lipids as fuel sources during submaximal exercise (e.g. Tarnopolsky *et al.*, 1990; but see Roepstorff *et al.*, 2002) or in the utilization of different lipid sources (Roepstorff *et al.*, 2002). Although the functional consequences of these differences in substrate metabolism are far from clear (Charkoudian and Joyner, 2004), it has been suggested that they would advantage women in endurance-related sports (Beneke *et al.*, 2005). Similarly, recent studies have suggested that women exhibit greater muscular endurance than men (e.g. Hunter and Enoka, 2001; Clark *et al.*, 2003; Gonzalez and Scheuermann, 2006; for contradictory results, see Ditor and Hicks, 2000; Gonzalez and Scheuermann, 2007). The exact origin of this dimorphism remains debated, but may be related to the fact that the greater absolute force generated by men causes a greater demand for muscle oxygen with more occlusion of blood flow due to increased compression of tissues (Clark *et al.*, 2003; Albert *et al.*, 2006). The differences between the sexes in the rate of fatigue development and recovery have been linked to the relative high performance of women in ultra-endurance sports (Speechly *et al.*, 1996; Bam *et al.*, 1997).

Clearly, many of the traits discussed above can be improved considerably by training. The response patterns of $\dot{V}O_{2\max}$, muscular strength, and endurance to both resistance and endurance training generally appear similar in both sexes (for a review, see Wells, 1991).

Reproductive hormones may play a major role in mediating many of the differences in morphology, physiology, and performance in men and women. Androgens (like testosterone) have anabolic (muscle-building) effects and influence practically every organ system in the adult body (Dabbs, 1992). Testosterone may also impact performance in many sports by its effect on the brain, for example by increasing spatial ability (Dabbs, 1992) or aggressiveness (Passelergue and Lac, 1999; but see Salvador *et al.*, 1999). The female reproductive hormones progesterone and oestrogen affect body temperature and heat dissipation rates (Stephenson and Kolka, 1999), ventilatory responses at high altitude (Regensteiner *et al.*, 1990), and metabolic substrate use (Zderic *et al.*, 2001).

With the exception of racehorses and greyhound dogs (P. Entin, in preparation), few studies have explored the proximate origins of sexual dimorphism in performance in other species of animals. It is unclear therefore whether the described differences in humans can be generalized. However, many of the differences concern morphological, physiological, and endocrinological systems shared by many vertebrates, so we do not see any reason to suspect that they would be unique to humans. The fact that so many aspects of the body related to physical performance exhibit sexual dimorphism begs an evolutionary explanation.

ULTIMATE CAUSES OF SEXUAL DIMORPHISM IN PERFORMANCE

Hinging on evolutionary theory regarding the origin and maintenance of sexual (size) dimorphism (see reviews in Hedrick and Temeles, 1989; Shine, 1989), ultimate explanations of sex differences in performance may imply natural selection, sexual selection, or both. Natural selection may act on male performance capacity as, for example, when locomotor or bite performance is important for survival in the face of predation. Predation risk may be higher in males than in females because males are more conspicuously coloured (e.g. Promislov *et al.*, 1992), and tend to expose themselves more often during mate searching (e.g. Shine, 1994) or territorial behaviours (e.g. Ryan *et al.*, 1982). Interestingly, male aquatic snakes of different evolutionary lines crawl (but do not swim) faster than conspecific females, possibly because males move over land more often in search of females (Scribner and Weatherhead, 1995; Shine *et al.*, 2003; Winne and Hopkins, 2006).

It has been argued that sexual differences in body size or morphology may also evolve for ecological reasons (Darwin, 1874; Schoener, 1967; Shine, 1989). According to the 'niche hypothesis', the males and females of a species may adapt to different microhabitats or diets to avoid competition. A textbook example of the niche divergence idea is the extraordinary bill dimorphism of the huia (*Heteraclocha acutirostris*), which likely arose as an adaptation to reduce inter-sexual food competition (Moorhouse, 1996). This idea equally applies to performance differences; if males and females occupy different niches, they may evolve different performance capacities. For instance, the female-larger sexual size dimorphism in raptorial birds may be a consequence of selection for greater aerial agility in males, an ability that would allow them to utilize a different foraging niche than the females [alternatively, it may be a product of sexual selection through female choice for more agile males in aerially displaying species (see Massemin *et al.*, 2000, for yet other hypotheses)]. Interestingly, in the anthropological literature, many scholars have linked the division of labour between the sexes in modern man to performance differences, arguing that hunting requires men's greater strength and speed more than other food-collecting tasks (e.g. Zihlman, 1981; Tanner, 1988; but see Balme and Bowdler, 2006). However, in humans and in many other species with sexual niche

divergence, it is difficult to separate cause and consequence. Sexual dimorphism may result from inter-sexual competition avoidance (or labour division), but niche divergence may also result as a by-product of sexual selection for size, shape, or performance.

In many groups of animals, fecundity selection contributes to differences in size and shape between the sexes (e.g. Braña, 1996; Preziosi *et al.*, 1996; Coddington *et al.*, 1997). It is likely that adaptations of the female body with respect to the production of offspring can also affect their physiological performance. For instance, the elongated abdomens of female lacertid lizards (relative to males), a possible outcome of fecundity selection for increased clutch volume (Braña, 1996), may limit their acceleration capacity (Van Damme and Vanhooydonck, 2002). In female turtles, the size of the pelvic opening may be under opposing selective forces, with wider apertures allowing passage of larger eggs, but possibly at the cost of locomotor and nest-building performance (Congdon and Gibbons, 1987). Especially in species where females carry eggs or developing young, the physical burden of the clutch may constrain locomotory abilities during pregnancy (e.g. Shine, 1980; Van Damme *et al.*, 1989), and the physiological changes associated with gestation may influence female running performance well beyond parturition (Olsson *et al.*, 2000). Reproductive hormones in females may orchestrate a shift in energy and nutrient allocation towards reproductive functions, at the expense of somatic functions (Rose and Bradley, 1998). Under the hypothesis of fecundity selection, sexual dimorphism in physiological performance among adult animals would result from a slower ontogenetic increase in performance in females, rather than from a sharper increase in males (as predicted by the sexual selection hypothesis).

Clearly, the most popular hypothesis for the origin of sexual dimorphism is sexual selection (Andersson, 1994). Intra-sexual selection seems an obvious explanation of sexual differences in physiological performance: males that excel in whole-animal functions such as speed, agility, and bite force may win more male combats and thus may leave more offspring. Although studies of intra-sexual selection have centred largely on morphological attributes used in combat, it is logical to assume that weapon performance will predict the outcome of fights better than weapon size or shape, and therefore should have stronger effects on fitness. Accordingly, in the polygynous territorial lizard *Crotaphytus collaris*, bite force is a better predictor of the fitness of males than head width (Lappin and Husak, 2005). Assuming that whole-animal performance reflects resource holding potential and genetic quality, both direct benefit and genetic models of inter-sexual competition predict selection on male performance traits. This may underlie the evolution of display behaviour involving elaborate physical activity (e.g. singing in birds and anurans, head-bobbing and push-ups in lizards).

A PRELIMINARY COMPARATIVE ANALYSIS OF SEXUAL PERFORMANCE DIMORPHISM IN LIZARDS

In what follows, we adopt a comparative approach to test hypotheses about the origin of sexual dimorphism in physiological performance in lizards. We first examine whether differences in size dimorphism correlate with sexual differences in performance. A positive correlation between performance and size dimorphism would confound further analyses, because it would not be apparent whether size or performance is the target of selection. Next, we relate among-species variation in sexual dimorphism of performance to differences in female reproductive effort. If females perform worse than males because fecundity selection has impaired their locomotor apparatus, then we expect to find a positive

correlation between measures of reproductive investment and performance dimorphism. Finally, we test whether territorial species exhibit better performance than non-territorial species, as predicted when males perform better than females because they are under stronger sexual selection for speed or endurance.

For several reasons, lizards are good model organisms to test hypotheses on the evolutionary origins of sexual dimorphism in performance capacity. First, lizards exhibit considerable interspecific variation in both direction and magnitude of sexual size dimorphism (Cox *et al.*, 2003). Second, species differ notably in reproductive investment (e.g. Shine, 1980) and mating systems (e.g. Stamps, 1977), allowing tests of the fecundity advantage and sexual selection hypotheses. Third, locomotor capacity in several lizards has been shown to be ecologically relevant, not only in the context of predator avoidance (e.g. Christian and Tracy, 1981; Le Galliard *et al.*, 2004; Miles, 2004) but also in social interactions (e.g. Perry *et al.*, 2004; Peterson and Husak, 2006; but see LeGalliard and Ferrière, 2008). Fourth, studies of lizard locomotion have a long tradition in ecological morphology and therefore there are probably more interspecific data on the running performance of lizards than for any other animal group (Bennett, 1980; Garland and Losos, 1994).

Locomotor performance data (maximal sprint speed and endurance) were taken from the literature and supplemented with our own data on lacertid and *Anolis* lizards (Table 1). Maximal sprint speed in lizards is typically measured by chasing individual animals along a racetrack, usually between 1.5 and 2 m in length. An individual's fastest performance over any 0.25- or 0.5-m interval over several trials (usually 3–5) is taken as a measure of its sprint capacity. Sprint speed is believed to be ecologically relevant, because many lizard species use short bursts of locomotion close to maximal capacity to elude predatory attacks, or during social interactions. Endurance is mostly measured by encouraging lizards to walk on a treadmill operating at moderate speed. Running time to exhaustion is considered an estimate of the lizard's endurance capacity. A lizard's stamina may index its ability to patrol territories, engage in energetically demanding displays, or contest vigorous fights. Details of the methodologies used to obtain performance measures vary among studies, but this is probably of minor importance here, since we are interested in the relative performance of the sexes. The mean speeds (or stamina) that were used to calculate sexual dimorphism in performance were always taken from the same study. Data from gravid females or individuals with broken tails were discarded. Sexual size dimorphism was calculated from data on male and female snout-to-vent lengths (SVL) in the literature (where possible, from the same source as the performance data). We used residual clutch mass [obtained by regressing $\log_{10}(\text{clutch mass})$ over $\log_{10}(\text{female SVL})$] as an estimate of reproductive effort. We crudely classified the species in the data set as 'territorial' or 'non-territorial' using the information compiled by Cox *et al.* (2003).

We performed all analyses with both conventional (ordinary least-square regression and analysis of variance) and phylogenetically informed techniques (through-origin regression of Felsenstein's independent contrasts and phylogenetic analysis of covariance) (Garland *et al.*, 1993). In the latter case, residual clutch mass was obtained by regressing contrasts of $\log_{10}(\text{clutch mass})$ on $\log_{10}(\text{female SVL})$ through the origin. As a phylogenetic hypothesis, we used the higher-level tree presented by Vidal and Hedges (2005), and supplemented it with data from the literature on the relationships within families [Scincidae (Brandley *et al.*, 2005; Austin and Arnold, 2006); Teiidae (Reeder *et al.*, 2002); Lacertidae (Arnold *et al.*, 2007); Polychrotidae (Nicholson *et al.*, 2005); Phrynosomatidae (Reeder and Montanucci, 2001)]. Because information on divergence times is scarce for most of these groups, we set all branch lengths equal to one.

Table 1. Sexual dimorphism in body size (SD_{ratio} , SVL), sprint speed (SD_{ratio} , speed), and endurance capacity (SD_{ratio} , endurance), and clutch mass (CLM) in different lizard populations and species

Species/population	SD_{ratio} SVL	SD_{ratio} speed	SD_{ratio} endurance	Reference	CLM	Reference
<i>Crotaphytus collaris</i>	1.13	1.04		Peterson and Husak (2006)	4.88	Vitt and Congdon (1978)
<i>Sceloporus merriami</i> (Boquillas)	1.05	1.16	1.27	Huey <i>et al.</i> (1990)		
<i>Sceloporus merriami</i> (Grapevine)	1.06	1.09	0.95	Huey <i>et al.</i> (1990)	0.99	Dunham (1981)
<i>Sceloporus occidentalis</i>	1.04	1.18	1.01	van Berkum <i>et al.</i> (1989)	3.28	Clobert <i>et al.</i> (1998)
<i>Urosaurus ornatus</i> (Big Bend, TX)	0.98	1.10	1.46	Miles (1994)	0.80	Dunham (1981)
<i>Urosaurus ornatus</i> (Big Wash Road, AZ)	1.00	1.13	0.57	Miles (1994)		
<i>Urosaurus ornatus</i> (Florida Wash, AZ)	1.02	1.15		Miles (1994)		
<i>Urosaurus ornatus</i> (Gardner Canyon, AZ)	1.07	1.25		Miles (1994)		
<i>Urosaurus ornatus</i> (Huachuca Mtns, TX)	1.01	1.17		Miles (1994)		
<i>Urosaurus ornatus</i> (Kickapoo Caverns, TX)	1.03	1.09	1.07	Miles (1994)		
<i>Urosaurus ornatus</i> (Lee's Ferry, AZ)	1.01	1.17	1.05	Miles (1994)		
<i>Urosaurus ornatus</i> (Mogollon Mtns, NM)	0.99	1.13	0.72	Miles (1994)		
<i>Urosaurus ornatus</i> (Molino Canyon, AZ)	1.05	1.08	1.30	Miles (1994)		
<i>Urosaurus ornatus</i> (Monticello, NM)	1.03	1.09		Miles (1994)		
<i>Urosaurus ornatus</i> (Saguaro National Monument, AZ)	1.09	1.13	1.21	Miles (1994)		
<i>Urosaurus ornatus</i> (Sevilleta National Wildlife Refuge, NM)	1.04	1.20	0.67	Miles (1994)		
<i>Urosaurus ornatus</i> (Sitting Bull Falls, NM)	1.02	1.18	0.48	Miles (1994)		
<i>Urosaurus ornatus</i> (Vernal, UT)	1.01	1.08	1.17	Miles (1994)		
<i>Urosaurus ornatus</i> (Water Canyon, NM)	0.98	0.94		Miles (1994)		
<i>Urosaurus ornatus</i> (Yuma, AZ)	0.96	1.24	0.45	Miles (1994)		
<i>Anolis angusticeps</i> (BH; Andros)	1.10	1.19		Our data		
<i>Anolis bahorucoensis</i>	1.18	0.79		Our data		
<i>Anolis barahonae</i>	1.10	1.49		Our data		
<i>Anolis brevirostris</i>	1.16	1.05		Our data		
<i>Anolis brunneus</i>	1.27	1.08		Our data		
<i>Anolis carolinensis</i>	1.28	0.93		Our data	0.43	Shine (1992)
<i>Anolis coelestinus</i>	1.32	1.13		Our data	0.19	Shine (1992)

Table 1.—(continued)

Species/population	SD _{ratio} SVL	SD _{ratio} speed	SD _{ratio} endurance	Reference	CLM	Reference
<i>Aspidoscelis</i> (' <i>Cnemidophorus</i> ') <i>gularis</i>	1.12	1.01		Paulissen (1998)	1.46	Vitt and Breitenbach (1993)
<i>Aspidoscelis</i> (' <i>Cnemidophorus</i> ') <i>inornatus arizonae</i>	0.98	1.03	1.54	Cullum (1998)		
<i>Aspidoscelis</i> (' <i>Cnemidophorus</i> ') <i>inornatus heptagrammus</i>	0.96	1.07	0.28	Cullum (1998)	0.65	Vitt and Breitenbach (1993)
<i>Aspidoscelis</i> (' <i>Cnemidophorus</i> ') <i>septemvittatus</i>	1.00	1.05	0.99	Cullum (1998)		
<i>Aspidoscelis</i> (' <i>Cnemidophorus</i> ') <i>sexlineatus</i>	0.95	1.23		Ballinger <i>et al.</i> (1979)		
<i>Aspidoscelis</i> (' <i>Cnemidophorus</i> ') <i>tigris marmoratus</i>	0.98	1.08	0.83	Cullum (1998)	2.28	Vitt and Breitenbach (1993)
<i>Aspidoscelis</i> (' <i>Cnemidophorus</i> ') <i>tigris punctilineatus</i>	1.07	1.03	1.15	Cullum (1998)	1.22	Vitt and Breitenbach (1993)
<i>Platysaurus intermedius</i>	1.11	1.15	1.00	Lailvaux <i>et al.</i> (2003)		
<i>Carlia rubrigularis</i>	1.12	0.98		Goodman (2006)	0.68	Goodman (2006)
<i>Eumeces chinensis</i>	1.10	1.09		Lin and Ji (2005)	9.64	Du (2004)
<i>Lampropholis guichenoti</i>	0.94	1.20		Shine (2003)	0.30	Qualls and Shine (1997)
<i>Niveoscincus metallicus</i>	0.99	1.17	1.48	Chapple and Swain (2002)	0.97	Swain and Jones (2000)
<i>Niveoscincus microlepidotus</i>	1.02	1.23		Olsson <i>et al.</i> (2000)		

Within species, males are faster than females (paired t -test, $t_{63} = 6.39$, $P < 0.001$), but males and females do not differ significantly in endurance ($t_{34} = -0.15$, $P = 0.88$). Sexual dimorphism in SVL does not correlate with dimorphism in speed ($r^2 = 0.045$, $n = 64$; Fig. 3A) or dimorphism in endurance ($r^2 = 0.016$, $n = 35$; Fig. 3B). Also, phylogenetically independent contrasts of SVL dimorphism do not correlate with contrasts of dimorphism in speed ($r^2 = 0.04$, $n = 63$) or endurance ($r^2 = 0.006$, $n = 34$). Residual clutch mass was a poor predictor of dimorphism in speed ($r^2 = 0.058$, $n = 23$; Fig. 3C) and dimorphism in endurance ($r^2 = 0.056$, $n = 14$; Fig. 3D). Accordingly, no significant relationships were found between the contrasts of residual clutch mass and those of dimorphism in speed ($r^2 = 0.057$, $n = 22$) or in endurance ($r^2 = 0.003$, $n = 13$). The mean (\pm standard error) sexual dimorphism in speed was $1.11 (\pm 0.17, n = 42)$ in territorial species and $1.06 (\pm 0.026,$

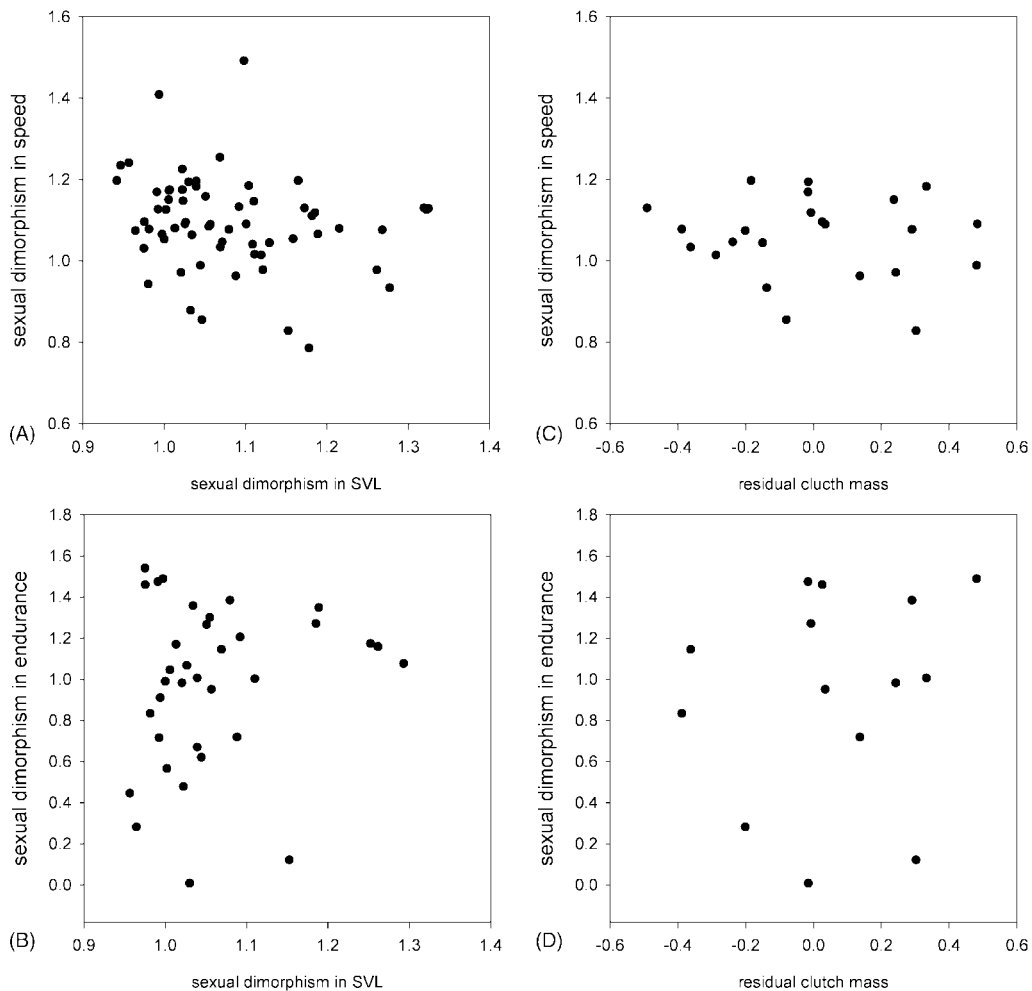


Fig. 3. Sexual dimorphism in sprint speed (A, C) and endurance (B, D) in relation to sexual size dimorphism (A, B) and female reproductive effort (C, D; residuals of the clutch mass–body size relationship) in different lizard species/populations.

$n = 22$) in non-territorial species. The F -value associated with this difference approaches significance when conventional F -tables are used ($P = 0.075$), but is far from significant ($P > 0.5$) when adequate tables generated using the phylogenetical model are used. This is clearly due to the fact that our score for territoriality was conservative at the family level. The mean dimorphism in endurance did not differ between territorial (1.00 ± 0.07 , $n = 18$) and non-territorial species (0.95 ± 0.11 , $n = 17$), with or without taking phylogeny into consideration (both $P > 0.5$).

These findings suggest that differences in speed or endurance between male and female lizards reflect sex-dependent selection on locomotor performance, and do not merely result from scaling laws and sexual size dimorphism. We find no evidence for the idea that different degrees of fecundity selection or intra-sexual selection may be responsible for the interspecific variation in sexual dimorphism in locomotor performance. We would like to stress, however, that these negative results could be due to the disparate nature of our data, most of which were gathered from studies with other aims. Future studies should address the intriguing phenomenon of sexual dimorphism in whole-animal performance by measuring sufficiently large samples of both males and females in a suitably close related group of species that exhibits variation in dimorphism, mating systems, and reproductive strategies.

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