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Correlates of ball size and rolling speed in the dung beetle *Kheper nigroaeneus* (Coleoptera: Scarabaeidae)

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Abstract

Ball rolling in dung beetles is an energy expensive activity associated with elevated thoracic temperatures. The ability of individuals to engage in such energetically costly behaviour may be dependent on their body condition. Bilateral asymmetries arising from the interaction between an individual's genes and its environment have been hypothesized to reflect an organism's quality. A number of studies have shown that individuals with elevated levels of asymmetry perform less well under stress. We tested this hypothesis by measuring correlates of dung ball rolling speed in males and females of *Kheper nigroaeneus* (Coleoptera: Scarabaeidae). We found that larger beetles produced larger dung balls and rolled them faster along an experimental track. However, there was no relationship between ball rolling speed and the asymmetry of fore and hind tibia. There was also no relationship between the asymmetry of the beetle or the number of mites that it carried, and the level of mite infestation did not influence ball rolling speed.

Key words: dung beetle, developmental instability, fluctuating asymmetry, performance, body size

INTRODUCTION

Natural selection favours individuals that perform fitness related activities efficiently. When such activities are particularly demanding in terms of energy, such as migratory flight, or agility required for escape responses, performance is likely to be related to the genotypic and phenotypic health, the 'condition', of the individual (Møller, 1994; Swaddle, 1997). Recently, condition has been inferred from measures of fluctuating asymmetry (Parsons, 1990, 1992), since the ability of an organism to maintain symmetry during development may reflect genetic stress, and the organism's ability to buffer the effects of environmental stress (Parsons, 1990, 1992).

Some recent studies have reported general relationships between developmental instability (as indicated by fluctuating asymmetry) and fitness (Møller, 1997; Møller & Thornhill, 1998; but see another meta-analysis by Leung & Forbes, 1996). Fluctuating asymmetry has also been correlated specifically with performance; for example, asymmetrical racehorses perform less well than symmetrical horses (Manning & Ockenden, 1994) and both barn swallows (*Hirundo rustica*; Møller, 1991) and red-billed streamertails (*Trochilus polytmus*; Evans, Martins & Haley, 1994) with asymmetrically manipulated tail streamers touched the walls of a flight maze more often than symmetrically manipulated individuals. Furthermore, the reduced manoeuvrability or stamina of asymmetric individuals has been shown to affect survival; flies (*Musca domestica*) with asymmetrical wings and legs are subject to higher predation by barn swallows (Møller, 1996) and by dung flies (*Scatophaga stercoraria*; Swaddle, 1997) and barn swallows with asymmetrical tails are more often captured by sparrow hawks (*Accipter nisus*; Møller & Nielsen, 1997).

The ball rolling dung beetle (*Kheper nigroaeneus*) constructs dung balls from ungulate dung (Edwards & Aschenbourn, 1989). Males construct large dung balls and wait for female beetles to arrive, rolling the ball away without assistance from the female who clings to the rolling ball. Females also construct and roll dung balls alone (Edwards & Aschenbourn, 1989). Ball rollers steer and roll the dung ball with their hind legs, whilst walking backwards with their fore legs. The fore and hind legs are therefore critical to the propulsion and direction of the ball. *Kheper nigroaeneus* exhibits extreme maternal care; a single offspring is produced from a brood ball and the female tends the larva for the 12 weeks that it takes to reach adulthood (Edwards & Aschenbourn, 1989).

Body size is frequently related to fecundity in female insects (Butlin & Day, 1985; Cook, 1988; Forbes & Baker, 1991) and to competitive ability in males (Heinrich & Bartholomew, 1979; Simmons, 1986; Ybarrondo & Heinrich, 1996). In dung beetles the size

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of the adult is largely determined by the amount of resources received by the larva (Emlen, 1994; Hunt & Simmons, 1997). Competition among beetles for dung is frequently intense (Heinrich & Bartholomew, 1979; Ybarrondo & Heinrich, 1996) and males often fight for possession of dung balls (Sato & Hiramatsu, 1993; Ybarrondo & Heinrich, 1996). This intensity of competition is, however, localized to the dung pad (Ybarrondo & Heinrich, 1996). Inter- and intraspecific competition at the dung pad will favour beetles that remove their dung balls swiftly (Heinrich & Bartholomew, 1979; Sato, 1998). Beetles may also suffer an increased risk of predation whilst constructing or rolling dung balls, again favouring beetles that can roll dung balls away and bury them quickly. A further cost of handling the dung ball above ground is kleptoparasitism by other dung beetle species, notably *Hyalonthophagus alcyonides* (pers. obs.; Ybarrondo & Heinrich, 1996). The extreme parental care exhibited in *K. nigroaeneus* makes avoiding such parasites particularly important. Under competition, ball construction time and ball volume are both reduced in *K. nigroaeneus* (Ybarrondo & Heinrich, 1996), further highlighting the importance of dung ball removal from the pad. Ball rolling is nevertheless an energy expensive activity and in *K. nigroaeneus* (Ybarrondo & Heinrich, 1996) and other scarabs (Heinrich & Bartholomew, 1979), is associated with elevated thoracic temperatures. Dung ball size and rolling speed are therefore likely to be associated with fitness.

Kheper nigroaeneus are frequently found to be infested with mites and several studies have demonstrated a decline in fitness associated with ectoparasitic infestation in other insect species (Abro, 1990; Forbes & Baker, 1991; Polak, 1993, 1997; Bonn *et al*., 1996). However, the relationship between ectoparasitism and phenotypic correlates of fitness, such as size or asymmetry, may not be a simple one. For example stress arising from ectoparasitic infestations of female *Drosophila nigrospiracula* is shown only by increased asymmetry in the sons of infected females (Polak, 1993). Furthermore, in holometabolous insects, larvae may not experience the same type or number of ectoparasites as the imago. Although the mites found on dung beetles are generally considered to be phoretic (Hanski & Combefort, 1991), they can occur in vast numbers around the mouth parts, eyes, and under the elytra, and conceivably present a significant pathology.

Here we evaluate the importance of body size, leg symmetry and ectoparasite load on the ball rolling performance of the dung beetle *K. nigroaeneus*.

METHODS

This study was carried out at Pullen Farm, the University of the Witwatersrand's field station near Nelspruit, Mpumalanga Province, Republic of South Africa. The experiment was conducted in open pasture in early November 1997. Fresh cattle dung was collected from the pasture and overnight kraals and placed in *c*. 2 litre pads every 2 m along a 100 m track. These dung pads attracted beetles and were checked continuously between 9:00 and 12:00. *Kheper nigroaeneus* that were rolling dung balls were collected and placed near the start of the course over which they were to be timed. The course was constructed from 2 parallel strips of cardboard 1.5 m long and 6 cm apart laid on a flat section of gravel road. The same section of road was used each day and all beetles rolled their dung ball in the same direction. The line at which the stopwatch was started was 30 cm along the course, ensuring that beetles were rolling at speed when timing began. The time taken for each beetle to roll its dung ball 1.2 m was recorded.

On completion of the trial, beetles and their dung balls were returned to the field station for measurement. The diameter of the dung balls and all of the morphometric measurements of the beetles (pronotum width and the length of the left and right fore and hind tibiae) were made using digital callipers. The entire sample of the beetles' fore tibia and a sub-sample of hind tibia from 18 beetles were measured twice to assess the repeatability of our asymmetry measurements. Eight beetles had damaged legs and these were recorded as such and not used in the asymmetry analysis. The beetles and their dung balls were weighed using a Mettler AC100 balance to the nearest 0.01g. The sex of all of the beetles was determined. The number of mites found on the cuticle of the beetle and under the elytra and wings was also recorded. Means are presented ± SE.

RESULTS

Body size and dung ball size

Of the 41 beetles collected, seven were males. Males tended to be larger than females, being significantly heavier, and having significantly longer fore tibia (Table 1). Males were rolling dung balls that were absolutely larger in diameter than female's dung balls (males, 40.68 ± 3.21 mm, females 34.29 ± 1.05 mm, $t = 2.341$, d.f. = 39, $P = 0.024$). However, after controlling for the difference in body size (by taking residuals from a regression of ball diameter on pronotum width), there was no difference between the relative sizes of the dung balls of males and females (mean residual dung ball diameter, males, 3.155 ± 2.79, females -0.65 ± 0.96, $t = 1.55$, d.f. = 39, NS). Across males and females there was a positive relationship between the diameter of the dung ball that the beetle was rolling and the pronotum width of the beetle (Fig. 1).

Fluctuating asymmetry (FA) analysis

The repeatability of our FA measurements was estimated using a repeated measures ANOVA. In both hind tibia and fore tibia the variance between individuals was significantly greater than the variance

Table 1. Mean ± SE of the body size traits of 7 male and 34 female *Kheper nigroaeneus*

	Male	Female	*t* (d.f. = 39)
Pronotum (mm)	18.15 ± 0.62	16.99 ± 0.25	1.86
Fore tibia (mm)	11.18 ± 0.42	10.09 ± 0.18	2.40*
Hind tibia (mm)	14.22 ± 0.47	13.43 ± 0.19	1.63
Mass (g)	2.14 ± 0.20	1.70 ± 0.73	2.35*

* $P < 0.05$.

Table 2. Mean ± SE asymmetry, kurtosis and skewness of fore and hind tibia of *Kheper nigroaeneus*

	n	Mean asymmetry	*t*	Kurtosis g2	Skewness g1
Fore tibia	36	−0.023 ± 0.014	1.601	1.123 ± 0.805	−0.768 ± 0.403
Hind tibia	36	0.029 ± 0.026	1.109	0.580 ± 0.805	−0.615 ± 0.403

between repeated measurements; (hind tibia, $F_{(15,17)} = 3.66$, $P = 0.005$, R (repeatability) = 0.55; fore tibia, $F_{(36,37)} = 3.48$, $P = 0.001$, $R = 0.57$).

The mean R–L asymmetry in both fore and hind tibia did not differ significantly from zero (Table 2) and there was neither significant skewness nor kurtosis in the R–L asymmetry distributions (Table 2), demonstrating that the traits show true fluctuating asymmetry. The mean |R–L| (absolute) asymmetries were 0.066 ± 0.01 in fore tibia and 0.121 ± 0.02 in hind tibia, less than 1% of leg length (fore tibia = 10.28 ± 0.18; hind tibia = 13.57 ± 0.18). A paired comparison (within beetles) revealed that after controlling for differences in tibia size by using relative FA (|R-L|/R+L/2), hind tibia were significantly more asymmetrical than the fore tibia (Wilcoxon signed ranks test $Z = 6.02$, $P < 0.05$). However, there was no relation between FA in fore and hind tibia (Spearman rank correlation, $r_s = 0.186$, $n = 33$, NS). Tibia asymmetry was unrelated to tibia length (fore tibia $r_s = 0.02$, $n = 37$, NS; hind tibia, $r_s = -0.10$, $n = 37$, NS) and

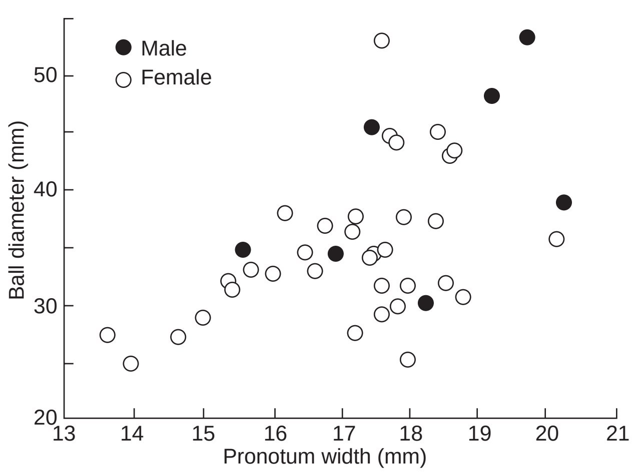

Fig. 1. The significant positive relationship between pronotum width and the diameter of the dung ball that the beetle was rolling (correlation coefficient = 0.497, $r^2 = 0.247$, $P < 0.001$).

Table 3. Relations between ball rolling speed (ms^{-1}) and tibia asymmetry (of intact beetles only) and mite load

	n	Spearman rank correlation
Number of mites	41	0.157
Fore tibia asymmetry	33	−0.001
Hind tibia asymmetry	33	−0.010

therefore absolute asymmetries were used in the analysis.

Correlates of ball rolling performance

Ball rolling speed was unrelated to the number of mites or to the absolute asymmetry in fore or hind tibia (Table 3); the only significant correlation was between pronotum width and speed (Fig. 2). Furthermore, there was no difference in ball rolling speed between beetles wwith intact legs and those whose asymmetry was elevated owing to breakage ($t = 1.0635$, d.f. = 39, NS).

There was no difference between males and females in their ball rolling speeds (males = 0.063 ± 0.01 m s^{-1}, females 0.062 ± 0.00 m s^{-1}, $t = 0.147$, d.f. = 39), and there were no effects of either ball mass (least squares regression, $b = -3.0 \times 10^{-4} \pm 3.4 \times 10^{-4}$, $F_{(1,39)} = 0.796$, NS) or ball diameter on rolling speed (LSR, $b = 2.2 \times 10^{-4} \pm 3.6 \times 10^{-4}$, $F_{(1,39)} = 0.387$, NS). Mites were not associated with increased asymmetry (fore tibia, $r_s = 0.165$, $n = 37$, NS; hind tibia, $r_s = 0.180$, $n = 37$, NS).

DISCUSSION

These results demonstrate that in the ball rolling scarab *Kheper nigroaeneus*, pronotum width is correlated with both the size of the dung ball and the speed at which the ball is rolled. This finding supports other studies which have found a positive relationship between body size in insects and measures of fitness such as female fecundity (Forbes & Baker, 1991), competitive ability (Heinrich & Bartholomew, 1979; Simmons, 1986; Ybarrondo &

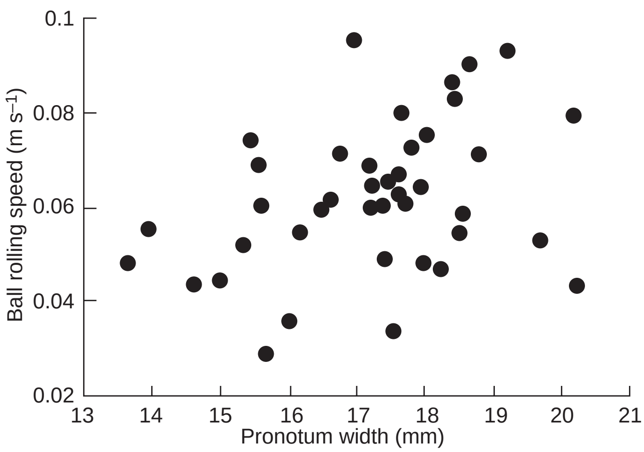

Fig. 2. The significant positive relationship between pronotum width and the speed at which the dung ball was rolled (correlation coefficient = 0.344, r^2= 0.118, $P < 0.05$).

Heinrich, 1996) and male mating success (Simmons, 1986; Gilburn, Foster & Day, 1992; Markow & Ricker, 1992; Simmons, 1995). The relation between body size and dung ball diameter in *K. nigroaeneus* may arise as a consequence of competition for dung balls: dung ball size is reduced under competition in *K. nigroaeneus* (Ybarrondo & Heinrich, 1996) and ball diameter may therefore reflect the competitive ability of the beetle. In fights over dung balls, the larger beetle tends to win (Heinrich & Bartholomew, 1979; Ybarrondo & Heinrich, 1996). Larger beetles, with less chance of loosing their ball to another beetle, might therefore construct larger dung balls than smaller beetles. However, two studies of *K. platynotus* (Sato & Imamori, 1987; Sato & Hiramatsu, 1993) have not found a relationship between dung ball size and pronotum width. One possible explanation for this apparent difference between species could be that the intensity of competition for dung is less in *K. platynotus*.

Fluctuating asymmetry in naturally selected traits such as legs is thought to be highly canalized (Møller, 1992; Balmford, Jones & Thomas, 1993) and the levels of asymmetry (< 1%) in the fore and hind tibia of *K. nigroaeneus* are typical of traits subject to natural selection (Soulé & Couzin-Roudy, 1982). The significantly lower asymmetry in the fore tibia suggests that the fore legs have been more strongly canalized with respect to fluctuating asymmetry. The importance of reduced asymmetry in the fore tibia may be due to their use in ball construction, or defence, since the fore but not hind legs are used in these activities (pers. obs.). However, neither the post-developmental asymmetries, nor the asymmetries arising from errors in development had an effect on ball rolling speed. It could be argued that the course over which the beetles ran was insufficiently challenging to reveal an influence of subtle asymmetries on performance. However, the fact that the course was sufficient to reveal how differences in the sizes of beetles influenced performance, strongly supports the notion that size is a better indicator of condition than asymmetry. Moreover, that gross post-development asymmetries had no influence on performance indicates how negligible any effect of fluctuating asymmetry would be. These findings are in contrast to the notion that subtle asymmetries either cause or are phenotypically linked to reduced performance under stress (Manning & Ockenden, 1994; Møller, 1996; Møller & Nielsen, 1997; Swaddle, 1997).

The number of mites carried by beetles did not correlate with ball rolling speed, suggesting that mites do not cause a significant deterioration in performance. Unfortunately we do not know if mite infestation in the adult reflects mite loads experienced by a larva, a situation that could result in increased fluctuating asymmetry; mite infestations in damselflies cause significant stress during a short period of time during adult eclosion, and reduced survival and elevated wing asymmetry (Bonn *et al.*, 1996). Our results suggest, however, that the mites do not cause significant stress to the beetle even when present in large numbers.

In conclusion, the most important determinant of dung ball size and rolling speed is pronotum width, whilst fluctuating asymmetry does not indicate the beetles' performance. This study supports the notion that body size but not asymmetry is a condition dependent trait in dung beetles.

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