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Sprint speed is not reduced by exaggerated male weapons in a flower beetle *Dicronocephalus wallichii*

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Abstract

Exaggerated sexually selected traits are assumed to decrease the mobility of bearers. However, previous empirical studies have often failed to support this assumption, possibly because locomotor performance represents the integration of numerous morphological, physiological and behavioural traits. Males of a flower beetle *Dicronocephalus wallichii* Pouillaude 1914 (Coleoptera: Scarabaeidae: Cetoniinae) possess elongated forelegs and a pair of exaggerated horns, which are used as dual weapons in male–male competition for mates. We investigated whether these two sexual traits impede the maximum sprint speed on bamboo branches with different angles and thicknesses under laboratory conditions. Our results suggested that no negative relationship exists between relative foreleg length or horn length and sprint speed. Elongated forelegs and horns may entail negligible locomotor costs. Males with longer horns and forelegs were found to have longer midlegs and hindlegs independent of body size. Thus, elongated midlegs and hindlegs in males may enhance balance, stabilize running on bamboo branches and compensate for the locomotor costs of bearing exaggerated weapons. Furthermore, a positive relationship was found between horn length and sprint speed on a horizontal branch. Males with longer horns probably have more energy and/or invest more heavily in appendage musculature. As is known in other animals, male horns of *D. wallichii* may act as honest indicators of body condition.

KEYWORDS
compensatory trait, flower chafer, honest signal, resource allocation, secondary sexual trait, sexual selection

1 | INTRODUCTION

Exaggerated male traits, including weapons and ornaments, have evolved in some cases under sexual selection (Andersson, 1994; Darwin, 1871). Although enlarged male traits increase the mating success of bearers, the same traits can be constantly subjected to stabilizing viability selection. This is because the development and maintenance of larger weapons and ornaments are associated with various fitness costs, such as increasing energetic demands, attracting predators and decreasing foraging efficiency (Andersson, 1994; Johnstone, 1995; Kotiaho, 2001). Studying the

costs of sexual ornaments and weapons is of central importance to our understanding of sexual selection theory for at least two reasons. First, the costs may oppose sexual selection, preventing any further enlargement of the traits. Consequently, the population will evolve optimal trait size towards an equilibrium point where survival costs and mating advantages are balanced (Kirkpatrick, 1982). Second, the reliability of ornaments and weapons as honest signals for male quality can be maintained by costs, given that the costs to a potential cheater (low-quality males) will be greater than those to an honest bearer (Grafen, 1990; Johnstone, 1995; Zahavi, 1975).

A major cost associated with exaggerated sexual traits is decreased mobility. Locomotor performance influences various aspects of individual fitness, including foraging, dispersal, reproductive success, defence of territories and predator evasion (Irschick, Meyers, Husak, & Galliard, 2008; Oufiero & Garland, 2007). In some species, exaggerated male traits have been shown to have negative effects on flight performance (stag beetle, *Cyclommatus metallifer*; Goyens, Wassenbergh, Dirckx, & Aerts, 2015) and swimming speed (swordtail, *Xiphophorus montezumae*; Kruesi & Alcaraz, 2007). However, because multivariate phenotypes can affect locomotor performance, the relationships between ornament or weapon size and locomotor performance are complex (Oufiero & Garland, 2007). Particularly, viability selection is expected to favour morphological traits that reduce the locomotor costs incurred by sexual traits (Husak & Swallow, 2011; Oufiero & Garland, 2007). Due to the effects of the compensatory traits, the locomotor cost is often difficult to detect (Allen & Levinton, 2007; Balmford, Jones, & Thomas, 1994; Baumgartner, Coleman, & Swanson, 2011; Buchanan & Evans, 2000; Evans & Thomas, 1992; Fowler-Finn, Rosenthal, & Hebets, 2013; McCullough, Weingarden, & Emlen, 2012; Møller, 1996; Oufiero et al., 2014). For example, relative horn length of a rhinoceros beetle *Trypoxylus dichotomus* was not related to flight speed (McCullough et al., 2012). Male beetles with larger horns have larger hindwings, which probably improves the flight ability of large individuals. Similarly, although eye stalks of male stalk-eyed flies increase the moment of inertia of the head, males perform as well as, or better than, females during aerial turning (Ribak & Swallow, 2007). A comparative analysis revealed that relative eye span of male stalk-eyed flies was positively related to relative wing span, suggesting the correlated selection of compensatory traits with the increased investment in sexually selected traits (Husak, Ribak, Wilkinson, & Swallow, 2011).

This study investigated the locomotor cost of male exaggerated traits in a horned flower beetle, *Dicronocephalus wallichii bourgoini* Pouillaude 1914 (Coleoptera: Scarabaeidae: Cetoniinae). Males of this species possess two sexually selected traits; a pair of horns on their heads and elongated forelegs (Figure 1a). Adults of this species aggregate in bamboo forests to mate and feed on the sap of young bamboo shoots. Males guard their mates from rival males after copulation. Guarding males engage in contests to defend mate ownership. Horns and forelegs are used in the early (i.e., assessment of resource holding potential of opponent) and escalated phase (i.e., physical battle) of the contests, respectively (Kojima & Lin, 2017). The males with larger horns and forelegs are more likely to win contests (Kojima & Lin, 2017). Males do not court females prior to copulation and females readily accept the males (Kojima & Lin, 2017). Therefore, the male exaggerated traits are thought to have evolved through male–male competition rather than female choice. Previous analyses of scaling relationships showed that the two weapons do not exhibit positive allometry (negative allometry for horns of large males and isometry for forelegs of any sized males; Kojima & Lin, 2017). The absence of positive allometry of weapons and sexual ornaments is generally interpreted by the consequences of net selection on the traits (i.e., viability selection and sexual selection;
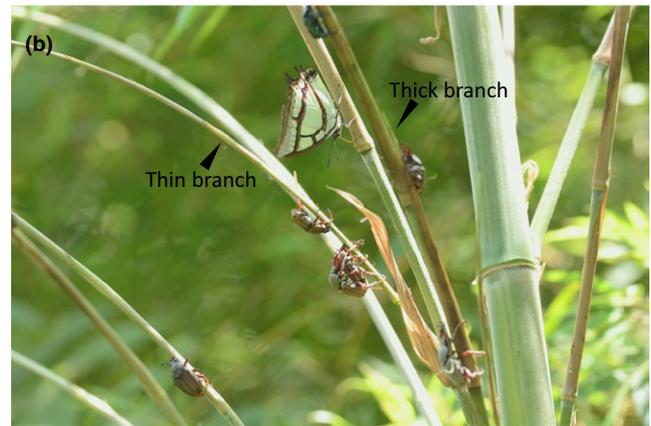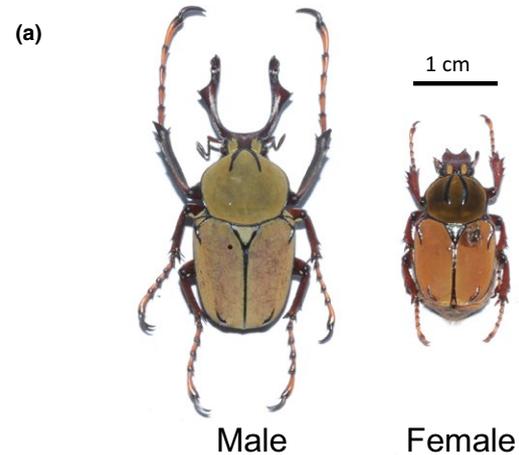

FIGURE 1 (a) A male and female *Dicronocephalus wallichii*. (b) *D. wallichii* feeding on bamboo sap in a natural habitat. The branches indicated by the arrows have almost the same diameters as the branches used in laboratory experiments (4 mm and 10 mm for thin and thick branches, respectively) [Colour figure can be viewed at wileyonlinelibrary.com]

Bonduriansky, 2007; van Lieshout & Elgar, 2009). However, the exact sources of the costs associated with sexual traits in *D. wallichii* remain elusive. To understand the evolution of exaggerated weapons in this species, it is crucial to elucidate the costs potentially associated with these traits.

Sprint speed can strongly influence the fitness of individuals of this species. A fast sprint would increase the survival rate when the beetle is attacked by predators, such as birds and tree lizards. Sprint is frequently observed in the context of mating in their habitat. For example, males chase after mates that escape during mate guarding (Kojima & Lin, 2017). Males often chase away rival males from their mates (Kojima & Lin, 2017). In addition, some males run towards a female while a guarding male of the female is fighting with other males (i.e., sneaking behaviour; Kojima & Lin, 2017). Elongated forelegs of *D. wallichii* should likely influence sprint speed, considering the functional link between forelegs and running. When walking or running on thin bamboo branch, *D. wallichii* uses mainly its tarsi (many segments, flexible to bend) rather than tibiae (one segment, no flexibility) for grasping the branch (Figure 1a; see Movies in Kojima & Lin, 2017). The larger

individual with longer forelegs either raise its body (higher centre of gravity) in order to use mainly the tarsi for grasping or with the same body position but use parts of the tibiae as points of contact to the branch. Therefore, we expect that the males with longer forelegs would make walking and running less balanced with their higher body positions and parts of tibia for grasping. We predicted that large forelegs have negative effects on the maximum running speed of *D. wallichii*. Male horns may also influence sprint speed in this species. Their horns are not so heavy, accounting for only 1.5–2.0% of the body mass (W. Kojima pers. obs.). However, given that male horns and mandibles of some scarab beetles including *Onthophagus taurus* (Moczek & Emlen 2000) and *Cyclommatus metallifer* (Goyens, Dirckx, & Aerts, 2015) impair locomotor performance (but see McCullough et al., 2012), the effects of horns of male *D. wallichii* on sprinting deserve examination.

In this study, we examined sprint speed of *D. wallichii* males on branches with different angles and thickness. The relationship between sprint speed and leg length of organisms is generally affected by diameters and angles of platforms (Losos & Irschick, 1996; Losos & Sinervo, 1989; Prenter, Fanson, & Taylor, 2012; Prenter, Pérez-Staples, & Taylor, 2010). For example, relatively long legs are predicted to be disadvantageous when sprinting on thin branches because the distance between centre of gravity and substrate will be increased, which reduces stability of walking (Losos & Sinervo, 1989; Pounds, 1988). Moreover, climbing requires alterations in the force production of each leg compared to horizontal running (Autumn et al., 2006; Goldman, Chen, Dudek, & Full, 2006). Thus, we expected that the disadvantages of having relatively long legs are prominent depending on the types of raceways in *D. wallichii* males.

On the other hand, the exaggerated weapons may not affect the sprint performance of *D. wallichii*, because the cost is offset by compensatory structures. Midlegs and hindlegs are good candidates for compensatory traits. Since males do not use midlegs and hindlegs in contests, these traits are unlikely to be sexually selected (Kojima & Lin, 2017). However, males of this species have relatively longer midlegs and hindlegs than the females (Kojima & Lin, 2017). Therefore, the elongated hindlegs and midlegs may be an adaptation to enhance balance and stabilize running. This study examined whether males with larger weapons sprint more slowly than males with smaller weapons, and whether males with larger weapons have longer midlegs and hindlegs, to explore the possibility of compensation for decreases in sprint performance.

2 | MATERIALS AND METHODS

2.1 | Insects

Ninety-four *D. wallichii* males were collected using an insect net in a lowland forest in the district of Tamsui, Taipei, Taiwan (25°11′N, 121°29′E) from May 16–30 of 2017. All beetles were intact and had six complete legs. The beetles were individually introduced to a 400-ml plastic cup within four hours of capture. The bottom of

the cup was covered with wet tissue, and the beetle was supplied with a piece of insect jelly sold commercially for rearing sap-feeding beetles. The cup was then kept in the incubator at 25 ± 0.5°C. The beetles were used for behavioural experiments one day later.

2.2 | Measuring sprint speed

The maximum running speed of male beetles was measured at a temperature of ca. 25°C in the laboratory during the daytime. Thick (10 mm in diameter and 80 cm in length) and thin (4 mm in diameter and 65 cm in length) straight bamboo branches collected from the study site were used as running platforms. The two branches were marked with oil-based ink at 1-cm increments.

The maximum sprint speed was measured using three types of raceways: a thin vertical branch, thick vertical branch and thin horizontal branch. The two branches with different thickness represent the young bamboo shoots and branches preferred in the wild (see Figure 1b and Kojima & Lin, 2017). The beetles are found on branches of various angles. The horizontal and vertical platforms we used represent two extreme conditions of angles. We did not use thick horizontal branches because such type of branches is uncommon in their habitat. For these treatments, the thin and thick branches were staged vertically by inserting their base in the soil, and a thin branch (the same branch as vertically inserted one) was positioned horizontally by inserting its base in a cardboard box. A male beetle was placed at the base of the branch, and its abdomen was gently stimulated by the fingers of the operator for 1 s to induce sprinting. Immediately after the beetle reached near the upper end, the beetle was placed back at the base of the same platform and the trial was repeated. A subsequent assay using a different raceway was conducted 20 min after the previous trials. The duration between different assays was probably sufficient for recovering the physical condition of the beetles (Herreid, Full, & Prawel, 1981). The order of three assays was assigned randomly. Running behaviour was recorded by a digital video camera (HDR-SR7; Sony, Japan) to measure speed. After the recording, the beetles were sacrificed in a freezer for subsequent morphological measurements.

The males usually continued to sprint on the branches for more than 30 cm without pausing. However, the time required during the initial 15-cm sprint was recorded, because our preliminary analyses showed that the speed gradually decreased after the first 15 cm and the male sprint distance rarely exceeds ~15 cm in nature (Kojima pers. obs., see also movies in Kojima & Lin, 2017). The fastest of the two consecutive trials was used in the subsequent analyses, thereby minimizing error derived from variation in motivation to run and suboptimal performance (Losos, Creer, & Schulte, 2002). The beetles that did not sprint more than 15 cm in at least one of the two trials were excluded from the analyses.

2.3 | Morphological measurements

The horn length (linear distance from base to tip), the pronotum width, and foreleg, midleg and hindleg length were measured as shown in

Figure S1 of Appendix S1 (Supporting Information). The pronotum width is generally used as an index of body size in scarab beetles (Emlen, 1997). The horn length and pronotum width were measured by a digital caliper (CD-15CPX; Mitutoyo, Japan) to the nearest 0.01 mm. Each right leg was dissected and fixed onto a sheet of white paper with cellophane tape. The legs were photographed, and their lengths from the femur to tarsus were measured using ImageJ software (https://imagej.nih.gov/ij).

2.4 | Statistics

All statistical analyses were performed using R version 3.0.1 (R Development Core Team, 2013). Pearson's correlation was examined among sprint speed on three raceways to assess the effect of angles and thicknesses on sprint speed. To examine the relationship between leg and horn length and sprint speed, we removed allometric effect of body size on leg/horn length by two methods. In the first analysis, we used residual leg/horn length regressed against body size as relative leg/horn length. However, the use of residuals is likely to produce biased estimates of test parameters (Freckleton, 2002; García-Berthou, 2001). In the second analysis, linear models (LMs) that incorporate the effect of body size to be removed as a covariate were used. This method is recommended in place of using residuals (Freckleton, 2002; García-Berthou, 2001), but when explanatory variables are highly correlated (i.e., multicollinearity), use of LMs also leads to variance inflation and increase in type 1 and type 2 errors (Graham, 2003; Zuur, Ieno, & Elphick, 2010). We assessed potential multicollinearity among explanatory variables by calculating variance inflation factors (VIFs) by R package *car*. VIFs were very large (7.8 < VIFs<20.69), suggesting high risk of yielding erroneous results (Graham, 2003; Neter, Kutner, Nachtsheim, & Wasserman, 1996). When we eliminated midleg length and hindleg length from full models, the collinearity was reduced but VIFs (7.2 < VIFs<10.53) were still larger than threshold of 2 (Graham, 2003) or 10 (Neter et al., 1996). Thus, although we adopted both residual and LMs methods to see whether they yield quantitatively similar results, we report in the main text the methods and results of residual analyses, and in Appendix S1 of the Supporting Information, the methods and results of full and reduced LMs.

The log-transformed foreleg, midleg and hindleg lengths were linearly regressed against the log-transformed pronotum width. The residual leg length was used as the relative leg length in the following analyses. A previous study showed that the regressed slope of log-horn length vs. log-pronotum width differed between large and small males (Kojima & Lin, 2017). Thus, the switch point and the coefficients of two linear regression lines were calculated following the formula presented by Kojima and Lin (2017). The residual horn length of the linear lines was used as the relative horn length.

To examine whether a negative relationship exists between relative weapon size and sprint speed, a linear model was used, in which sprint speed on the thin vertical, thick vertical or thin horizontal branches was a dependent variable and relative horn length and relative foreleg, midleg and hindleg length were explanatory variables. The log-transformed pronotum width was also included as a covariate to control the effect of body size on sprint speed. The potential multicollinearity among explanatory variables was tested using VIFs. In order to test the compensatory hypothesis, Pearson's correlation was examined among relative length of horns, forelegs, midlegs and hindlegs.

3 | RESULTS

3.1 | Sprint speed on three types of raceway

The maximum sprint speed by males showed high repeatability between the two consecutive trials for all three assays ($r > 0.81$, $p < 0.001$, t test). Sprint speed on the thick vertical branch was significantly correlated with that on the thin vertical branch ($r = 0.49$, $t = 5.17$, $p < 0.001$, Figure 2) and that on the horizontal branch ($r = 0.26$, $t = 2.40$, $p = 0.019$, Figure 2). The correlation between sprint speed on the horizontal branch and thin vertical branch was not significant ($r = 0.17$, $t = 1.54$, $p = 0.13$).

3.2 | Weapon size and sprint speed

We analysed the relationship between weapon size and sprint speed by residual method and LMs. Here, we report the results of residual
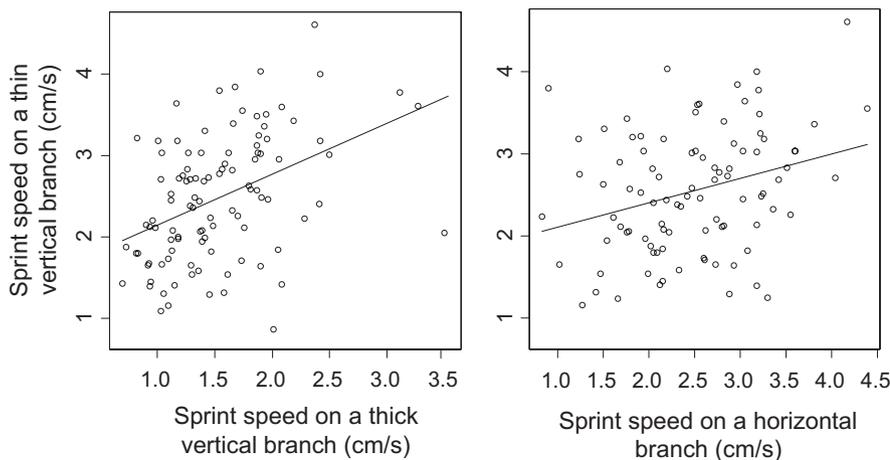

FIGURE 2 Relationships between sprint speed on a thin vertical branch and sprint speed on a thick vertical branch (left) or a horizontal branch (right) in *Dicronocephalus wallichii* males

method. Although caution is required in interpretation the statistical results (Freckleton, 2002; García-Berthou, 2001), both residual and LM methods yield identical results (see Supporting Information Appendix S1 for LMs).

The allometry analysis of horn and body sizes revealed a switching point (see Eberhard & Gutierrez, 1991; Kojima & Lin, 2017) of the regressed slope at 0.98 (9.55 mm) of pronotum width. The regressed slope was 2.78 and 1.79 for small males (<9.55 mm of pronotum width) and large males (≥9.55 mm of pronotum width), respectively.

In all models, VIFs were below 2.9, suggesting the absence of severe collinearity. Thus, all explanatory variables were included in all models. For assays with the thick vertical, thin vertical and horizontal branch, 0, 8 and 10 out of 94 males failed to continuously sprint more than 15 cm in at least one of the two trials. They were excluded from analyses, but this unlikely biases our results because sizes of the morphological traits (three leg length, horn length and body size) of the failed males were not significantly

different from those of males that sprinted more than 15 cm ($p > 0.29$, Welch t test).

There was not a significant relationship between relative foreleg length and sprint speed on any raceways. Relative horn length was positively significantly and marginally significantly related to sprint speed on the horizontal branch (Figure 3, Table 1, $p = 0.016$) and thick vertical branch (Figure 3, Table 1, $p = 0.065$), respectively, but not on the thin vertical branch (Table 1). Midlegs, hindlegs and pronotum width were not related to the sprint speed on any raceways (Table 1) except for on thin vertical branch in which relative hindleg length was positively related to sprint speed (Figure 4, Table 1, $p = 0.0074$).

3.3 | Correlation between morphological traits

All morphological traits (i.e., relative horn length, relative foreleg length, relative midleg length and relative hindleg) were significantly inter-correlated (Figure 5a,b, Table 2, $p < 0.001$).
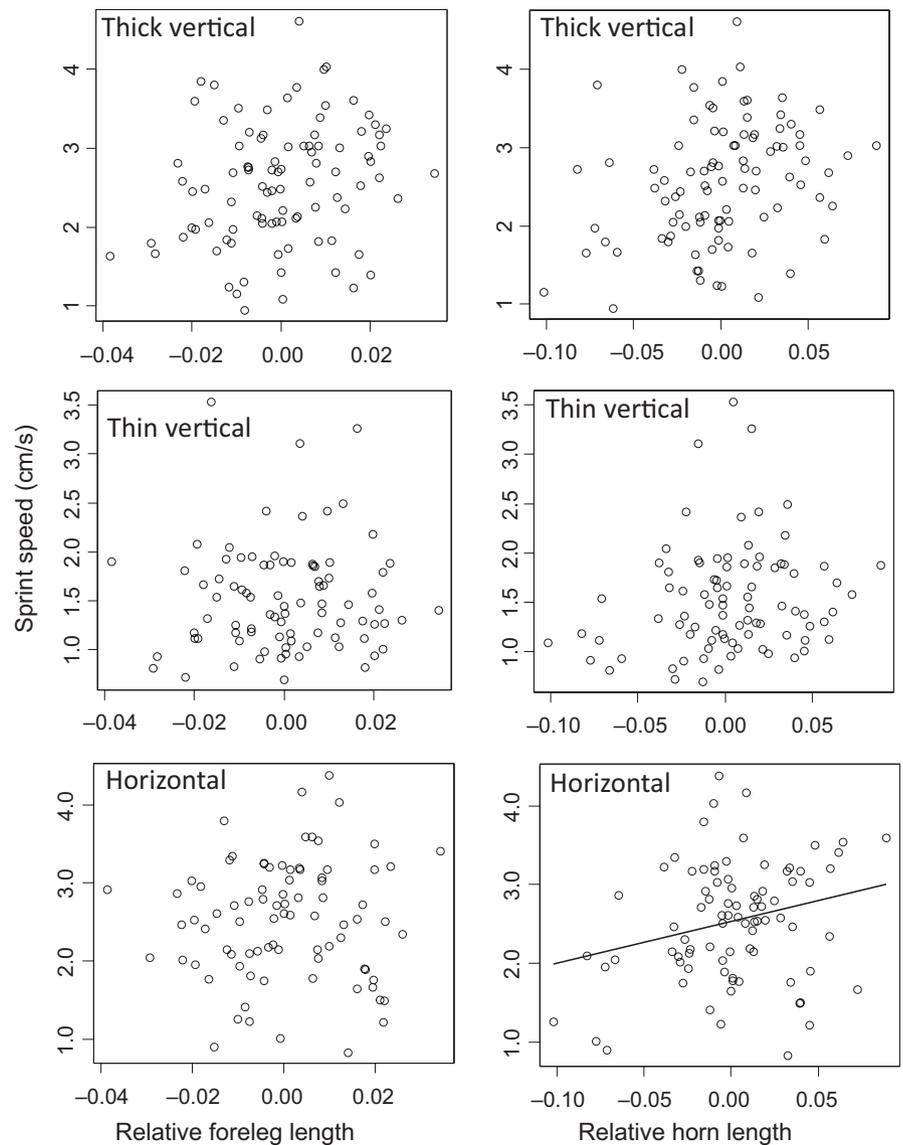

FIGURE 3 Relationships between male weapon size (relative horn length and relative foreleg length) and maximum sprint speed on a thick vertical branch, a thin vertical branch and a horizontal branch in *Dicronocephalus wallichii* males. A regressed line is shown for a statistically significant relationship

Raceway type	Explanatory variable	Coefficient	SE	t	P
Thick vertical branch	Intercept	−1.35	2.17	−0.62	0.54
	Relative foreleg length	4.61	9.08	0.51	0.61
	Relative midleg length	−6.91	7.42	−0.93	0.35
	Relative hindleg length	5.90	8.03	0.73	0.46
	Relative horn length	5.05	2.71	1.87	0.065
	Pronotum width	4.00	2.22	1.80	0.075
Thin vertical branch	Intercept	3.20	1.60	2.00	**0.048**
	Relative foreleg length	−11.7	6.74	−1.74	0.086
	Relative midleg length	−6.48	5.49	−1.18	0.24
	Relative hindleg length	16.4	5.97	2.75	**0.0074**
	Relative horn length	3.26	1.99	1.63	0.11
	Pronotum width	−1.68	1.63	−1.03	0.31
Horizontal branch	Intercept	1.15	2.30	0.50	0.619
	Relative foreleg length	−13.9	9.58	−1.46	0.150
	Relative midleg length	−2.91	7.89	−0.37	0.714
	Relative hindleg length	8.64	8.57	1.01	0.317
	Relative horn length	7.21	2.92	2.47	**0.016**
	Pronotum width	1.44	2.35	0.61	0.541

Note. Significant effects ($p < 0.05$) are highlighted in bold.

4 | DISCUSSION

Although theories assume that development and maintenance of larger weapons are associated with various fitness costs (Grafen, 1990; Kirkpatrick, 1982), we found no empirical support for the locomotor costs of exaggerated head horns and elongated forelegs in *D. wallichii* males. The elongated forelegs of *D. wallichii* did not have a negative impact on maximum sprint speed in any assays with branches of different angles and thickness. This result is counterintuitive, because sexual selection is expected to have extended the length of forelegs beyond their locomotor optimum. Alternatively, the costs of male weapons in *D. wallichii* may be simply negligible. Especially, this may be the case for horns. The metabolic or biomechanical costs of carrying weapons are probably varied depending on the relative mass of them. The proportion of horn mass of *D. wallichii* to body mass was much smaller than that of claws of a fiddler crab *Uca pugilator* (50%, Allen & Levinton, 2007) and mandibles and musculature of a stag beetle *Cyclommatus metallifer* (18%, Goyens, Dirckx, et al., 2015) in which locomotor costs have been found, but as much as that of horns of a rhinoceros beetle *Trypoxylus dichotomus* (1.5%, McCullough et al., 2012) in which locomotor costs were not detected.

Additionally, there are two possible explanations for the absence of a negative relationship between weapon size and sprint speed. First, the cost of elongated forelegs may be obscured by the confounding factors. Locomotor performance of insects is affected by various factors including health, age and developmental conditions (Frazier, Harrison, Kirkton, & Roberts, 2008; Gibert, Huey, & Gilchrist, 2001). The beetles used in the present study were caught in the field, and therefore, these variables were not controlled in the trials. Second, the cost of sexually selected traits may be compensated by the modifications of other traits. Compensation for locomotor cost has been reported in various animals. For example, males of a rhinoceros beetle *T. dichotomus* have larger hindwings than females, and males with a relatively longer horn have relatively larger hindwings, which probably compensates for the cost of bearing a larger horn in flight (McCullough et al., 2012). In
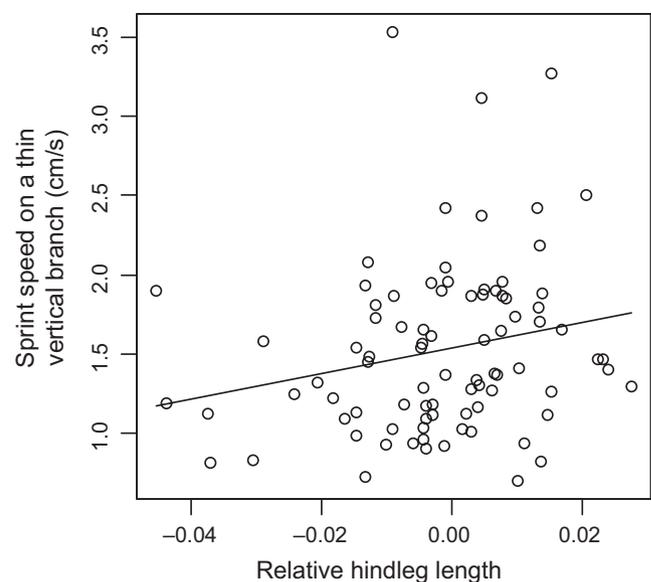

FIGURE 4 Relationship between relative hindleg length and maximum sprint speed on a thin vertical branch in males of *Dicronocephalus wallichii*
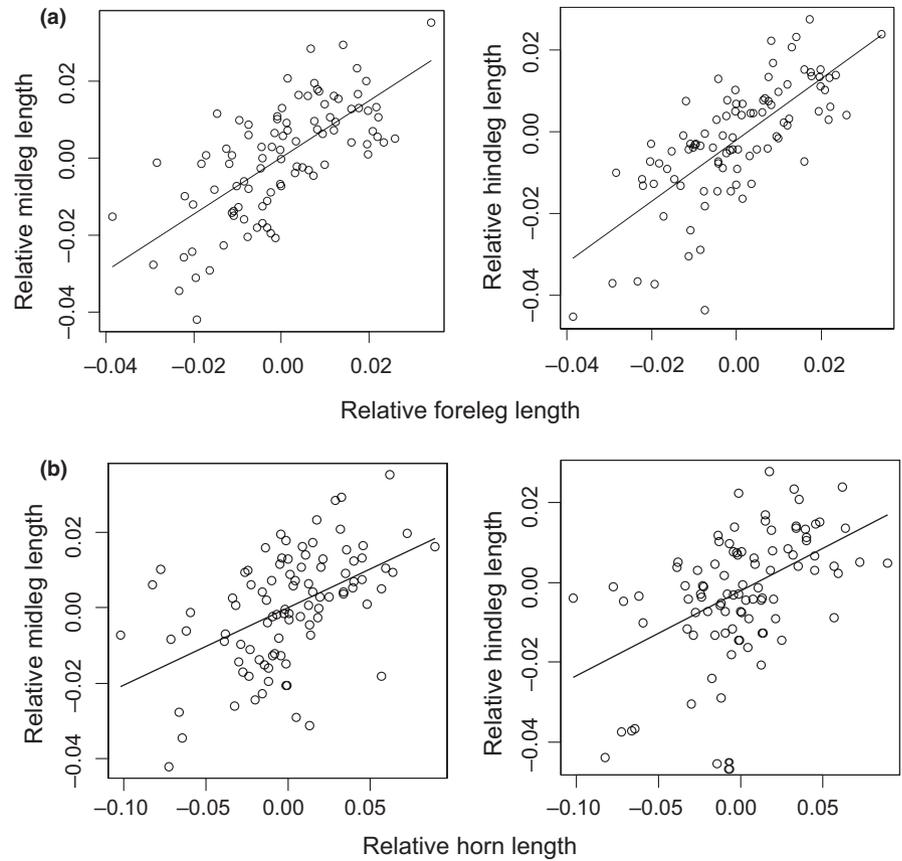
FIGURE 5 Relationships between relative foreleg length (a) or relative horn length (b) and relative midleg length (left) or relative hindleg length (right) in *Dicronocephalus wallichii* males

TABLE 2 Pearson correlation coefficients between male morphological traits of *Dicronocephalus wallichii*. All correlations were statistically significant (*p* < 0.001)

	Relative horn length	Relative foreleg length	Relative midleg length	Relative hindleg length
Relative horn length	1.00	0.61	0.49	0.52
Relative foreleg length	—	1.00	0.69	0.73
Relative midleg length	—	—	1.00	0.66
Relative hindleg length	—	—	—	1.00

D. wallichii, males are known to have longer midlegs and hindlegs than females after controlling for body size (Kojima & Lin, 2017). These elongated midlegs and hindlegs in males probably enhance stable running. Indeed, in the present study, a positive relationship was found between relative hindleg length and sprint speed on a vertical thin branch. Furthermore, relative foreleg and horn length was positively correlated with relative midleg length and hindleg length. These findings support the compensatory hypothesis.

The positive correlation between weapon size and leg length has been reported in other coleopteran insects including a rhinoceros beetle *T. dichotomus* (McCullough & Emlen, 2013) and a giraffe weevil *Lasiorhynchus barbicornis* (Painting & Holwell, 2013). Alternative

to compensatory hypothesis, the positive associations among traits can be explained by two hypotheses. Firstly, the traits may represent correlated morphological adaptations for fighting. If longer legs help males to resist attacks from opponents and to elevate their bodies on top of opponents during contests (Goyens, Dirckx, et al., 2015; Okada, Suzaki, Miyatake, & Okada, 2012), the selection for longer horns and legs would be correlated due to advantages in fighting. Secondly, the positive relationship between weapon size and other morphological traits may be a by-product of physiological development or pleiotropy rather than adaptation (Painting & Holwell, 2013) given that the development of morphological traits in an organism is controlled in an integrated manner.

The positive correlation between leg length and horns may suggest that there is no resource competition among these traits. Although trade-offs in resource allocation have been found in many insects including rhinoceros beetles *Dynastes* spp. (Kawano, 1995), stag beetles (Kawano, 1997) and dung beetles *Onthophagus* spp. (Emlen, 2001; Moczek & Nijhout, 2004), this and other recent studies have shown that resource trade-off is not a universal trend among animals with sexually selected weapons and ornaments (McCullough & Emlen, 2013; Painting & Holwell, 2013; Schwab & Moczek, 2014). On the other hand, the positive correlation may be explained by the "big houses, big cars" hypothesis, in which when there is a large variation in resource acquisition, but not in resource allocation to all aspects of their life histories, positive correlation would appear among life-history traits (Reznick, Nunney, & Tessier, 2000; Van Noordwijk & de Jong, 1986). Thus, the positive correlation among life-history traits does not necessarily suggest the absence of trade-off among traits.

Our finding that there was no relationship between any leg length and sprint speed on any substrate (with the exception between hindleg length and sprint speed on thin vertical branches) is inconsistent with the results of studies in taxa other than insects. A comparative study in *Anolis* lizards showed that long-legged species ran faster than short-legged species on thick branches, whereas short-legged species had much less difficulty than long-legged species in moving on thin branches (Losos & Sinervo, 1989). Similarly, males of an orb-web spider *Argiope keyserlingi* with relatively short legs were found to have a performance advantage when climbing on substrates of small diameter, whereas males with relatively long legs climbed faster on substrates of large diameter (Prenter et al., 2010). The advantages of short-legged individuals on thin substrate were not found in the flower beetle we studied, which is probably attributable to the different kinetics of locomotion among taxa with different number of legs. However, we are unaware of any previous studies investigating the relationship between climbing speed and diameter of substrates in insects.

A positive relationship between relative horn length and sprint speed on a horizontal branch was found in the present study. This indicates that males that invest more in the development of horns may have more energy and/or invest more in the musculature of appendages. Furthermore, if sprint speed reflects overall quality or vigour (Oufiero & Garland, 2007), males with longer horns may have a better body condition. Sprint speed is likely to influence the probability of winning contests because *D. wallichii* males chase away rival males during contests (Kojima & Lin, 2017). If so, male horns could act as an honest indicator of fighting ability. A positive relationship between weapon size and locomotor performance has also been found in a horned dung beetle, *Euoniticellus intermedius*. Males of *E. intermedius* with relatively larger horns have higher running endurance (Lailvaux, Hathway, Pomfret, & Knell, 2005).

In conclusion, no costs associated with the two *D. wallichii* male weapons during sprinting were detected in this study, possibly due to the effects of compensatory traits (e.g., elongated midlegs and hindlegs) or the negligible costs of the weapons. This study examined maximal sprint speed, but not other parameters of locomotor performance including stability, cost of transport and energetics during sprint and flight that were found to be affected by weapon size in other species (Allen & Levinton, 2007; Goyens, Dirckx, et al., 2015; Husak et al., 2011). For example, detailed morphometrics and kinematics revealed that males of a stag beetle *Cyclommtus metallifer* with extremely large mandibles are statically instable, which probably impairs locomotion (Goyens, Dirckx, et al., 2015). Such mechanical approaches would be also informative to understand the locomotor costs in *D. wallichii*. Since the locomotor performance of an organism generally represents the integration of numerous morphological, physiological and behavioural traits (Ghalambor, Walker, & Reznick, 2003; Oufiero & Garland, 2007), determining the effect of a specific trait on locomotor performance is complicated. Researchers have tackled this problem in multiple ways, including the experimental manipulation of sexual traits (Allen & Levinton, 2007; Basolo & Alcaraz, 2003; Baumgartner et al., 2011; Evans & Thomas, 1992; Gerald & Thiesen, 2014; Møller, 1989), using novel phenotypic variation of hybrids (Johnson, Macedo, Passow, & Rosenthal, 2014), comparative analyses (Balmford et al., 1994; Husak et al., 2011, 2013; Oufiero et al., 2014) and simulation with computational fluid dynamics (Goyens, Dirckx, et al., 2015; Goyens, Wassenbergh, et al., 2015). These multilevel approaches would provide important information on potential locomotor costs of weapons and on the compensatory mechanisms associated with the costs in this species.

CONFLICT OF INTEREST

The authors have no conflict of interests to declare.

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