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Lifting Capacity of Horned Passalus Beetles During Passive and Stressed States

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Abstract Many beetle species engage in territorial behaviors or male-male contests involving lifting or flipping their opponents, although this type of strength has never been empirically quantified. This study examined the lifting capacity of a medium-sized (1–2 g) saprolytic beetle native to the United States (horned passalus beetle, *Odontotaenius disjunctus*), and strength was measured during passive and stressed states. Twenty beetles were individually placed in a 'push-up' position with a force sensor on their backs and allowed to lift continuously for 2 min without manipulation, and then for another 2 min with a mild stress stimulus applied (tapping the elytra with a probe). The unmanipulated peak force readings during the first half were surprisingly high (up to 5 N, or 500 g), based on prior experiments examining the pulling strength of this species (indicating they can pull up to 100 g), but in nearly all beetles their peak lifting power in the stressed state increased by an average of 87 %. There was a positive relationship between strength measurements in both passive and stressed states. This appears to be the first empirical demonstration of the lifting capacity of a beetle, and these results also have considerable implications for the study of physical performance in beetles and other animals, especially in cases where maximum exertion data are of interest.

Keywords Behavioral states · horned passalus beetles · lifting strength · *Odontotaenius disjunctus*

Introduction

Relative to their size, beetles are some of the strongest creatures in the animal kingdom. For example, a male dung beetle (*Onthophagus taurus*) can pull over 1,000 times its own body weight (Knell and Simmons 2010) and Dor beetles (family Geotrupidae) can move loads that weigh 400 times their body mass (Klausnitzer 1981). Less spectacular (but still impressive) is the horned passalus beetle (*Odontotaenius disjunctus*), a 1–2 g beetle that lives in rotting logs in eastern North America, which can pull approximately

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50 times its own weight (Davis et al. 2013). Regardless of the species, most work on beetle strength involves attaching thread harnesses to them and either measuring how much weight (or force) they can pull, or how much force it takes to pull them backwards or upwards to mimic their ‘tunnel holding ability’ (e.g. Lailvaux et al. 2005; Benowitz et al. 2012). However, lifting power is also important for beetles, since in many beetle species, including the horned passalus beetle, mating or territorial fights can involve one individual lifting or flipping its opponent with its horn(s) or mandibles (Hongo 2003; Wicknick and Miskelly 2009). Despite this, lifting strength has never been empirically quantified in any beetle species.

Whether it is strength measurements in beetles, or sprint speed in lizards, the assessment of physical performance in animals often involves obtaining the maximum value, or the animal’s ‘peak’ physical performance in standardized trials (Garland et al. 1995; Losos et al. 2002; Husak et al. 2006). This may be for convenience or for statistical purposes (i.e. to obtain a single number for each individual). However, if the measurement is passive (i.e. the animal is unmanipulated), results for all individuals may not be accurate because of variation in motivation (Losos et al. 2002). This may be overcome if a mild stimulus is applied, such as gentle prodding to stimulate locomotion (e.g. Garland et al. 1995; Tejedo et al. 2000). To the author’s knowledge, the actual magnitude of the difference (if any) between performance measures of passive versus stimulated animals has never been quantified.

The current study was undertaken to evaluate the lifting strength of the horned passalus beetle and to compare its lifting strength to its pulling strength, which is known from prior work (Cox and Davis 2013; Davis et al. 2013). Lifting strength was assessed in an unmanipulated state and when a mild stress stimulus was applied to ensure maximal motivation and to allow for comparisons of performance between the two behavioral states.

Methods

Beetle Sources This study used two sets of beetles collected during November 2012 from different locations in Georgia (Athens and Savannah, GA, n=8 and n=12, respectively). Beetles were collected by hand from decaying logs and brought to the lab where they were kept in captivity in 20 L glass (Athens) or plastic (Savannah) containers (filled with rotting hardwood) for 2 months prior to force trials. There was no significant difference in size (live weight) of beetles from the two sites (mean= 1.70 g, Student’s t-test, df=18, t=−1.47, p=0.156).

Measuring Lifting Force On the day of testing (all tests were done on 31 January 2013 between 1 and 5 pm) beetles were individually removed from their container and immediately placed on a wooden block between two insect pins that held them in place (at the constriction between prothorax and abdomen), but still allowed them to lift their bodies upward, as in a ‘push-up’ movement (Fig. 1, inset). The wooden block with the beetle was then positioned under a force sensor equipped with a flat plate that just touched the top of the beetle’s head and prothorax (Fig. 1). In all cases, this took between 10 and 20 s from the time the beetle was picked up. Most beetles immediately began pushing upward at this point, and this force was recorded by the sensor (in

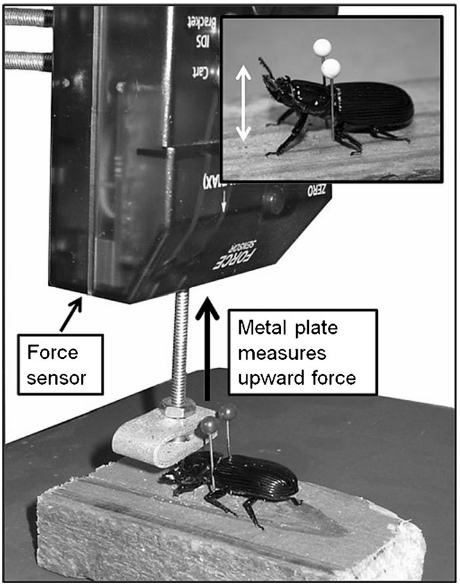

Fig. 1 Measurement of beetle lifting force. Beetles were positioned on a wooden block using insect pins placed on either side (inset figure), and were positioned under a force sensor that recorded the continuous lifting force produced at the head and prothorax region (see Fig. 2 for force readings)

Newtons). Those beetles that did not push upward were removed from the experiment. The sensor was connected to a data-logger, so that the upward force of the beetle could be measured continuously (10 readings per second) over time.

Once in position and once force data began recording, the beetles were not manipulated for 2 min. At the 2-min mark, and for the final 2 min, a stress stimulus was continuously applied: a blunt probe was used to gently tap on the elytra (dorsal surface of the abdomen) every 2 s. A prior experiment by the author (unpublished) showed how this action elicits alarm calls, which this species makes by rubbing an abdominal tergite rasp against an area on the ventral side of each folded metathoracic wing (Buchler et al. 1981). In that experiment, ten beetles were placed on the same wood block with the same pin arrangement, and monitored for alarm calls for 4 min, with the same stimulus applied during the last 2 min. Seven of the beetles made no sounds during the first 2 min, the remaining three made between 25 and 125 alarm calls. The number of alarm calls of all beetles significantly increased (by a factor of four) when the stimulus was applied (paired t-test, $df=9$, $t=-6.27$, $p=0.0001$). During the strength trials described in this paper, most beetles responded similarly, although their calls were not recorded. For all beetles, their unmanipulated lifting force was measured first, followed by the stress treatment. It was not possible to randomize the order of these procedures because of the temporal nature of the insect stress response, which can last 15–30 min (Davenport and Evans 1984). If the stress treatment was performed first, the beetles would remain stressed during the unmanipulated portion of the trial.

Data Analysis For each beetle the maximum force readings for both the first 2 min (without stimulation, ‘time 1’) and the second 2 min (with stimulation, ‘time 2’) were retained as the measures of lifting strength. Maximum force at time 1 and time 2 were both normally-distributed. A repeated-measures ANOVA was used to determine the effect of stimulation on maximum lifting force (at time 1 vs time 2), with collection site included as a predictor variable (Athens vs Savannah). The effect of beetle size (weight) on lifting power (either at time 1 or time 2) was also examined using Pearson Correlations, as was the relationship between beetle mass and strength.

Results and Discussion

The maximum lifting power without stimulation (i.e. during the first 2 min) across all beetles was 2.2 N (±1.09SD) and ranged from 0.49 to 4.98 N. During the second 2 min (with stimulation), the average maximum force reading was 3.38 N (±1.16SD) and ranged from 0.83 to 6.28 N. The repeated-measures ANOVA showed the effect of time (time 1 vs. time 2) was significant ($F_{1,18}$=26.21, p<0.0001); average lifting force increased when the beetles became stressed. This increase in lifting force could be seen in 18 of 20 beetles time 2 force measurements (Table 1). Force readings from a typical beetle are displayed in Fig. 2, along with the average readings for all 20 beetles. In nearly all beetles there was an immediate and sharp increase in lifting force as soon

Table 1 Summary of live weights and maximum force measurements for all passalus beetles examined in this study. All force readings are in Newtons (1 N=101 g)

Beetle #	Population	Weight(g)	Time 1	Time 2	% Change
1	Athens	1.08	1.54	0.84	−45.6
2	Athens	1.60	1.19	3.49	+193.2
3	Athens	1.63	1.54	1.73	+12.3
4	Athens	1.65	3.44	2.49	−27.6
5	Athens	1.65	1.92	4.11	+114.1
6	Athens	1.67	2.84	3.82	+34.3
7	Athens	1.69	1.11	2.11	+90.2
8	Athens	1.93	2.03	3.17	+56.0
9	Savannah	1.44	0.92	2.82	+205.9
10	Savannah	1.53	1.73	3.22	+85.9
11	Savannah	1.61	2.33	3.60	+54.6
12	Savannah	1.62	2.63	3.87	+47.4
13	Savannah	1.62	3.19	4.55	+42.4
14	Savannah	1.66	3.30	3.55	+7.4
15	Savannah	1.77	1.33	3.82	+187.7
16	Savannah	1.91	3.14	3.68	+17.2
17	Savannah	1.92	0.49	3.14	+544.4
18	Savannah	1.93	3.22	4.79	+48.7
19	Savannah	2.05	1.71	2.52	+47.6
20	Savannah	2.11	4.98	6.28	+26.1
Average		1.70	2.23	3.38	+87.1

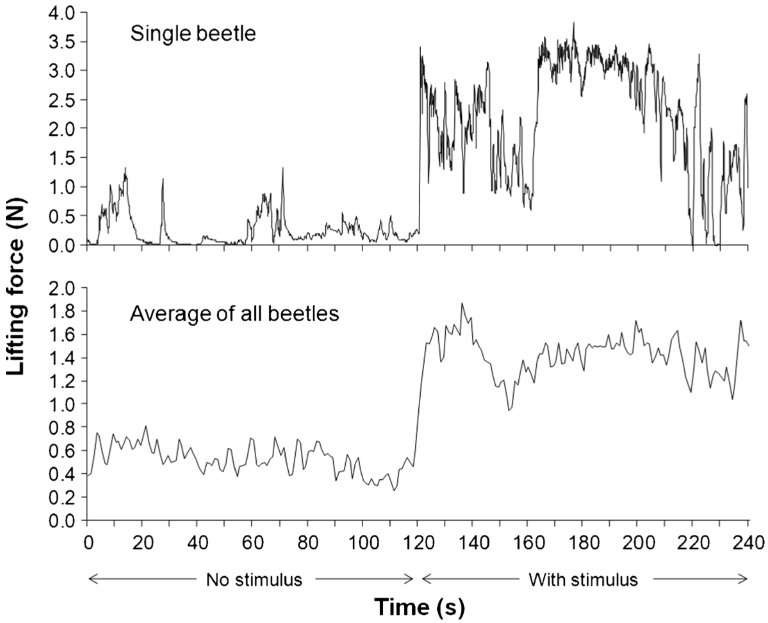

Fig. 2 Lifting force measurements over time for one beetle (*top*) and for all 20 beetles in this experiment (*bottom*). Bottom graph shows average force readings of all beetles every second. Error bars not displayed for clarity. Note the difference in scale between both graphs. All trials lasted 4 min, and beetles were not manipulated during the first 2 min. For the last 2 min, the hind end was gently and continuously tapped with a blunt probe

as the stimulation was applied (Fig. 2). This was usually accompanied by alarm calls, which continued for the remainder of the trial. The ANOVA results showed an effect of collection site that approached significance ($F_{1,18}$=3.07, p=0.0967), but no significant interaction between time and site ($F_{1,18}$=2.25, p=0.150).

Despite the effect of stimulation on lifting strength, the maximum force at time 1 (without stimulation) was positively related to the maximum force at time 2 (with stimulation; r=0.64, p=0.0023, Fig. 3). There was no effect of beetle mass on max force at time 1 (r=0.343, p=0.138) but a positive relationship at time 2 (r=0.566, p=0.0093).

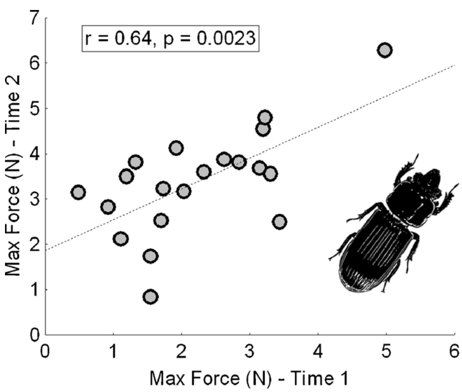

Fig. 3 Relationship between maximum force reading at time 1 (without stimulation) and at time 2 (with stimulation) for all beetles

There were a number of findings from this experiment that are important for understanding the behavior of this and other beetle species, but also for the researcher interested in measuring strength in beetles and other animals. The first is the surprising lifting capacity of this beetle even without stimulation. These beetles (which all weighed between 1 and 2 g) appeared to be capable of lifting approximately 2.2 N or 224 g on average. This is over twice as much as a prior estimate of its maximum pulling strength, which was approximately 100 g on average, and obtained without stimulation (Davis et al. 2013). Given that fighting in many beetles can involve lifting and flipping opponents, this behavior may have played an important role in the evolution of body design (placement of muscles, size of legs, etc.).

When a stress stimulus was applied to the beetles their lifting capacity increased by an average of 87 % (Table 1). The maximum force reading during time 2 was lower than in time 1 in only two individuals (see Table 1). Moreover, there were some beetles that had a relatively strong initial force readings (between 3 and 5 N), and even these beetles pushed harder still when stressed. This is also supported by the positive relationship between force at time 1 versus time 2 (Fig. 3). It is clear then, that most beetles were not exerting their true 'maximum strength' during the passive part of the experiment, even if they appeared to be exceptionally strong individuals.

From a physiological standpoint, the increase in lifting force after stimulation could be interpreted as a manifestation of the fight-or-flight response, which is universal among vertebrates and invertebrates, and involves stimulation of muscles, redirecting energy from non-essential processes and preparing the animal for extreme physical exertion (Adamo 2008). This effect would be adaptive in repelling predatory attacks as well as during aggressive encounters with other beetles. Support for this second idea comes from prior observations of this species showing that aggressive encounters are usually accompanied by loud stridulations (alarm calls) which increase in frequency as the intensity of the encounter increases (Mullen and Hunter 1973).

Finally, the novel approach used in this study to measure beetle strength could be used for a variety of future research projects focusing on beetle performance. These could include comparisons with other strength measures important for beetles, such as grip strength (Stork 1980; Benowitz et al. 2012). It would also be of interest to know if lifting performance is associated with morphological characteristics of beetles known to index fitness, such as horn size (Emlen et al. 2012). The possible effect of parasites on lifting performance could also be examined (Cox and Davis 2013). Regardless of the direction, researchers should bear in mind the results shown here that emphasize how measures of maximum exertion depend on the behavioral state of the organism.

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References

Adamo SA (2008) Norepinephrine and octopamine: linking stress and immune function across phyla. Invertebr Surviv J 5:12–19

Benowitz KM, Brodie ED III, Formica VA (2012) Morphological correlates of a combat performance trait in the forked fungus beetle, *Bolitotherus cornutus*. PLoS ONE 7(8):e42738. doi:10.1371/journal.pone.0042738

Buchler ER, Wright TB, Brown ED (1981) On the functions of stridulation by the passalid beetle *Odontotaenius disjunctus* (Coleoptera, Passalidae). Anim Behav 29:483–486

Cox D, Davis AK (2013) Effect of a parasitic nematode, *Chondronema passali* Leidy (*Incertae Sedis*), on the size and strength of the horned passalus, *Odontotaenius disjunctus* Illiger (Coleoptera: Passalidae). Coleopt Bull 67(2):1–7

Davenport AP, Evans PD (1984) Stress-induced changes in the octopamine levels of insect hemolymph. Insect Biochem 14(2):135–143

Davis AK, Attarha B, Piefke TJ (2013) Measuring the strength of horned passalus beetles (*Odontotaenius disjunctus*): revisiting an old topic with modern technology. J Insect Sci 13:107

Emlen DJ, Warren IA, Johns A, Dworkin I, Lavine LC (2012) A mechanism of extreme growth and reliable signaling in sexually selected ornaments and weapons. Science 337(6096):860–864

Garland T, Gleeson TT, Aronovitz BA, Richardson CS, Dohm MR (1995) Maximal sprint speeds and muscle-fiber composition of wild and laboratory house mice. Physiol Behav 58(5):869–876

Hongo Y (2003) Appraising behaviour during male-male interaction in the Japanese horned beetle *Trypoxylus dichotomus septentrionalis* (Kono). Behaviour 140:501–517

Husak JF, Fox SF, Lovern MB, Van Den Bussche RA (2006) Faster lizards sire more offspring: sexual selection on whole-animal performance. Evolution 60(10):2122–2130

Klausnitzer B (1981) Beetles. Simon and Schuster, New York

Knell RJ, Simmons LW (2010) Mating tactics determine patterns of condition dependence in a dimorphic horned beetle. Proc R Soc B 277(1692):2347–2353

Lailvaux SP, Hathway J, Pomfret J, Knell RJ (2005) Horn size predicts physical performance in the beetle *Euoniticellus intermedius* (Coleoptera : Scarabaeidae). Funct Ecol 19(4):632–639

Losos JB, Creer DA, Schulte JA (2002) Cautionary comments on the measurement of maximum locomotor capabilities. J Zool 258:57–61

Mullen VT, Hunter PE (1973) Social behavior in confined populations of the horned passalus beetle (Coleoptera: Passalidae). J Georgia Entomol Soc 8(2):115–123

Stork NE (1980) Experimental analysis of adhesion of *Chrysolina polita* (Chrysomelidae: Coleoptera) on a variety of surfaces. J Exp Biol 88:91

Tejedo M, Semlitsch RD, Hotz H (2000) Covariation of morphology and jumping performance in newly metamorphosed water frogs: effects of larval growth history. Copeia 2000(2):448–458

Wicknick JA, Miskelly SA (2009) Behavioral interactions between non-cohabiting bess beetles, *Odontotaenius disjunctus* (Illiger) (Coleoptera: Passalidae). Coleopt Bull 63(1):108–116