

## RESEARCH ARTICLE

# A disparity between locomotor economy and territory-holding ability in male house mice

Jeremy S. Morris\*, James S. Ruff, Wayne K. Potts and David R. Carrier

## ABSTRACT

Both economical locomotion and physical fighting are important performance traits to many species because of their direct influence on components of Darwinian fitness. Locomotion represents a substantial portion of the total daily energy budget of many animals. Fighting performance often determines individual reproductive fitness through the means of resource control, social dominance and access to mates. However, phenotypic traits that improve either locomotor economy or fighting ability may diminish performance in the other. Here, we tested for a predicted disparity between locomotor economy and competitive ability in wild-derived house mice (*Mus musculus*). We used 8 week social competition trials in semi-natural enclosures to directly measure male competitive ability through territorial control and female occupancy within territories. We also measured oxygen consumption during locomotion for each mouse using running trials in an enclosed treadmill and open-flow respirometry. Our results show that territory-holding males have higher absolute and mass-specific oxygen consumption when running (i.e. reduced locomotor economy) compared with males that do not control territories. This relationship was present both before and after 8 week competition trials in semi-natural enclosures. This disparity between physical competitive ability and economical locomotion may impose viability costs on males in species for which competition over mates is common and may constrain the evolution of behavioral and phenotypic diversity, particularly in natural settings with environmental and resource variability.

**KEY WORDS:** Male–male aggression, Cost of transport, Functional trade-offs, Sexual selection, Whole-organism performance

## INTRODUCTION

Whole-organism performance is dependent upon a variety of integrated physiological traits. Because performance often directly determines aspects of Darwinian fitness, functional constraints on performance may limit phenotypic and life-history evolution. Many phenotypic traits that ultimately determine performance may be under conflicting selective pressures because of incompatible performance demands. For example, both economical locomotion and physical fighting play key roles in many aspects of the life history and ecology of animals. However, phenotypic traits that improve either locomotor economy or fighting ability may conflict with performance in the other (Carrier, 2002; Oufiero and Garland, 2007), resulting in a functional trade-off (Lewontin, 1978; Maynard Smith et al., 1985; Lauder, 1991; Vanhooydonck et al., 2001; Van

Damme et al., 2002) whereby simultaneous specialization for both activities is impossible. Compromises resulting from such trade-offs may be vital to understanding the evolution of behavioral and phenotypic diversity in many species (Arnold, 1992).

Locomotion represents a substantial portion of the total daily energy budget of many animals (Altmann, 1987; Kenagy and Hoyt, 1989; Karasov, 1992; Chappell and Dlugosz, 2009; Rezende et al., 2009). Locomotor economy is an important performance trait because of its direct influence on energetics. For example, reduced locomotor economy and the resulting higher energetic demand may impose viability costs in the manner of increased foraging time, increased exposure to predation and decreased free energy for growth, maintenance, reproduction or other behaviors (Blanckenhorn, 2000). Likewise, fighting has profound effects on individual fitness because it often determines control of resources and access to mates (Andersson, 1994). Male reproductive success is frequently linked to traits that improve fighting ability and social dominance, such as larger body mass (Clutton-Brock et al., 1982; Le Boeuf and Reiter, 1988), larger weapon size (Preston et al., 2001; Coltman et al., 2002; Kruuk et al., 2002), greater bite force (Huyghe et al., 2005; Husak et al., 2009) and greater agility (Lailvaux et al., 2004).

Functional trade-offs between locomotor economy and fighting ability are likely to exist for a variety of physiological and biomechanical reasons (Carrier, 2002). Specialization for economical locomotion is associated with elongation of the limbs, which decreases the number of locomotor cycles to travel a given distance as well as the required rate and amplitude of muscle force generation (Gambaryan, 1974; Hildebrand, 1985; Kram and Taylor, 1990), and reduced distal limb mass, which decreases the energy required to cycle the limbs (Hildebrand and Hurley, 1985; Steudel, 1990). In direct contrast to these traits, specialization for fighting appears to result in stout body plans, greater muscle mass in the distal limbs (Pasi and Carrier, 2003), high mechanical advantages about the limb joints (Morris and Brandt, 2014; Morris and Carrier, 2016), and increased safety factors (Alexander, 1981) in the limb bones to resist high loading in variable directions that may occur during aggressive interactions (Kemp et al., 2005). These contrasting phenotypes may lead to a performance disparity between economical locomotion and fighting ability.

Previous studies examining relationships between locomotor performance and sexually selected performance traits have provided mixed results. Studies on lizards have shown both increased (Garland et al., 1990; Robson and Miles, 2000; Perry et al., 2004; Husak et al., 2006) and decreased (López and Martín, 2002) locomotor performance (sprint speed and/or stamina) with social dominance or reproductive success and with characters improving competitive ability (e.g. bite force and head size; Cameron et al., 2013). In fact, many studies have found that certain individuals outperform others in all tasks, a phenomenon that has invoked a recent surge in research on the concept of ‘individual quality’ (Van

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Received 13 December 2016; Accepted 25 April 2017

Damme et al., 2002; Wilson and Nussey, 2010; Lailvaux and Kasumovic, 2011; Wilson et al., 2014). However, few studies have been carried out examining similar performance traits in mammals and no study to our knowledge has examined the relationship between resource holding potential (e.g. individual fighting ability; Parker, 1974) and locomotor economy. In combination with previous work on ectothermic species, the inclusion of studies on mammals will lead to a broader understanding of whole-organism performance and the importance of specific performance traits. Additionally, given the central role of energetics in physiological ecology (McNab, 2002), there is a need for the incorporation of potential energetic trade-offs into performance studies (Lailvaux and Husak, 2014).

In house mice (*Mus musculus*), the importance of fighting ability for increasing reproductive fitness as well as the high daily costs of locomotion are expected to generate selection on these two potentially conflicting performance traits. House mice have a polygynous mating system in which territory control among males is determined by frequent and intense fighting, resulting in a high incidence of injury and even death (Brown, 1953; DeVries et al., 1997; Demas et al., 1999). Though biting is the major mode of inflicting damage, fighting between mice also involves grappling, rolling and pushing, as well as lunging toward (aggressively) or jumping away from (defensively) an opponent (Miczek et al., 2001). Together, these data indicate that fighting in house mice involves dynamic actions and is dependent upon multiple aspects of morphology and physiology (i.e. whole-organism performance; Lailvaux and Irschick, 2006). Likewise, house mice are dependent on locomotor performance for frequent travel in order to forage and to patrol and scent-mark territories, as well as when dispersing to new areas (Latham and Mason, 2004). Home ranges of feral house mice range from 235 m<sup>2</sup> in open fields (Quadagno, 1968) to 6000 m<sup>2</sup> in forests (Fitzgerald et al., 1981). Typical foraging behavior includes an average of 200 small meals per night, spread out between 20–30 food sites (Meehan, 1984), in order to meet a daily food intake of up to 20% of body mass (Berry, 1970; Meehan, 1984). Additionally, mice may cover large distances (>1.5 km) when dispersing (Berry, 1968). Though data are not currently available for daily travel distance in wild house mice, laboratory mice furnished with a voluntary running wheel cover an average of 4.4 km per day (up to 11.6 km per day with artificial selection; Koteja et al., 1999) and expend 26–28% of total daily energetic output on locomotion (Rezende et al., 2009).

Based on the functional anatomy and physiological arguments above, we expect territory-holding (TH) male mice to have reduced locomotor economy compared with non-territory-holding (non-TH) males. To test this, we used three separate populations of 10 male and 16 female unrelated age-matched adult mice in 8-week semi-natural enclosure trials to directly measure male territory control and female occupancy within territories. Genetic parentage analyses of mice populations in the experimental system used in this study have shown that territory control is a proxy for male reproductive fitness, with TH males siring approximately 80% of all offspring (Carroll et al., 2004). In addition, for each mouse, we measured the rate of oxygen consumption ( $\dot{V}_{O_2}$ ) at intermediate running speeds and used both  $\dot{V}_{O_2}$  (ml O<sub>2</sub> min<sup>-1</sup>) and mean mass-specific oxygen consumption per unit distance (ml O<sub>2</sub> g<sup>-1</sup> km<sup>-1</sup>; Taylor et al., 1970, 1982) as measures of locomotor economy. For these running trials, we used open-flow respirometry in an enclosed treadmill across a small range of speeds centered on the preferred voluntary running speeds of house mice (15–25 m min<sup>-1</sup>; Rezende et al., 2006). Oxygen consumption at the mid-range of running speeds has

been shown to be highly correlated with the overall cost of transport (general equation across all aerobic speeds; Taylor et al., 1982). We conducted running trials both before and after semi-natural enclosure trials. These methods allowed us to determine: (i) whether there is a difference in locomotor economy between TH and non-TH male house mice; and (ii) whether this difference is a result of being in a competitive environment (i.e. from a decrease in performance associated with stress, injury, exhaustion or temporary hormonal surges that may occur during semi-natural enclosure trials).

## MATERIALS AND METHODS

### Study population and design

Mice (*Mus musculus* Linnaeus 1758) used in our study were from an established wild-derived colony (Meagher et al., 2000) that has been managed to maintain genetic diversity similar to that of wild populations (Cunningham et al., 2013). A major advantage of using wild-derived mice is that they retain wild behaviors that are often lost in both inbred and outbred laboratory strains (Koide et al., 2000; Nelson et al., 2013b). Three separate populations of 10 male and 16 female unrelated age-matched (55±3.7 weeks old) adult mice were communally housed in 30 m<sup>2</sup> (similar to wild population densities; Sage, 1981) semi-natural enclosures (Fig. S1). These enclosures simulate natural habitat complexity and provide easily defended abundant resources. This is consistent with natural settings in which territorial strategies are common (Sage, 1981; Latham and Mason, 2004) and have been found to induce normal behaviors in wild mice (e.g. Potts et al., 1991; Manning et al., 1992; Meagher et al., 2000; Ilmonen et al., 2008). All enclosures were located within the same facility, with controlled ambient temperature (16–20°C) and photoperiod (12 h light:12 h dark). Mice were kept in this facility for the duration of the experiment. Prior to entering into the experimental protocol, all mice were individually housed for at least 2 weeks and were socially naive (had not previously lived in a socially competitive environment). All protocols were approved by the Institutional Animal Care and Use Committee of the University of Utah (Protocol 14-05010).

### Social competition trials

Passive integrated transponder (PIT) tags (TX1400ST, BioMark, Boise, ID, USA) implanted in each mouse and PIT tag readers (FS2001F-ISO, BioMark) at each feeder allowed real-time monitoring of social structure (individual occupancy and territorial control). Enclosure trials lasted 8 weeks with minimal human disturbance. At the conclusion of enclosure trials, PIT tag reader data were analyzed. Males were designated as TH if they successfully controlled a territory with a minimum of two females (i.e. a polygynous territory) for at least 3 continuous weeks. Territory control was defined as a given male excluding all other males from a territory, such that >80% of all male PIT tag reads were for that given male. Males that never reached this degree of territory control were designated as non-TH (adapted from Nelson et al., 2013a; Ruff et al., 2013).

### Locomotor trials

Running trials were conducted both before and after competition trials. During running trials and for 2 weeks (pre-enclosure) or 24 h (post-enclosure) prior, mice were individually housed (food and water *ad libitum*) to control for any previously existing differences in food or water consumption, injury, exhaustion or temporary hormone surges. Mice were not handled when being transferred between cages and the treadmill in order to minimize any stress from human contact.

Day 1 was for treadmill training and consisted of the following 5 min intervals: acclimation ( $0 \text{ m min}^{-1}$ ),  $8 \text{ m min}^{-1}$ ,  $12 \text{ m min}^{-1}$ , recovery ( $0 \text{ m min}^{-1}$ ),  $16 \text{ m min}^{-1}$  and  $20 \text{ m min}^{-1}$ . Day 2 was a rest day. On day 3,  $\dot{V}_{\text{O}_2}$  data were collected using the following protocol: 5 min acclimation, 10 min warm-up at  $12 \text{ m min}^{-1}$ , 5 min recovery, 10 min trial at  $16 \text{ m min}^{-1}$ , 5 min recovery, 10 min trial at  $20 \text{ m min}^{-1}$ . Day 4 was a rest day. On day 5, data were collected using the following protocol: 5 min acclimation, 10 min warm-up at  $12 \text{ m min}^{-1}$ , 5 min recovery, 10 min trial at  $24 \text{ m min}^{-1}$ .

Trials were carried out on a fully enclosed airtight AccuPacer Mouse Treadmill (volume  $2300 \text{ ml}$ ; Omnitech Electronics, Inc., Columbus, OH, USA) with a clear top panel.  $\dot{V}_{\text{O}_2}$  was measured via open-flow respirometry. Flow rate through the running chamber was maintained at  $750 \text{ ml min}^{-1}$  using mass flow meters (Model M-10, Sierra Instruments, Monterey, CA, USA), which ensured that oxygen concentrations within the chamber remained above 20.5%. Subsamples were drawn (at  $100 \text{ ml min}^{-1}$ ) from the excurrent air flow, scrubbed of  $\text{CO}_2$  (soda lime), dried of water vapor (Drierite) and analyzed for  $\text{O}_2$  concentration using  $\text{O}_2$  analyzers (Model S-3A, AEI Technologies, Pittsburgh, PA, USA; FoxBox Respirometry System, Sable Systems International, Las Vegas, NV, USA). Because these  $\text{O}_2$  analyzers have different response times, we used different lag times for analysis. Otherwise, the respirometry setup for each analyzer was identical. We verified that each analyzer obtained equivalent results for  $\text{O}_2$  response using controlled flows of nitrogen gas. Analyzers were used simultaneously and randomly with respect to individuals and running speeds. Data were collected at 5 Hz using a Biopac MP100 (Biopac Systems, Inc., Goleta, CA, USA) and analyzed using LabAnalyst software (Warthog Systems, www.warthog.ucr.edu). All trials were conducted during the first half of the dark cycle, corresponding to the highest activity period of mice (Rhodes et al., 2003). Body mass was measured after each running trial.

$\dot{V}_{\text{O}_2}$  for each running speed was calculated as:

$$\dot{V}_{\text{O}_2} = \dot{V} \times (F_{\text{I}\text{O}_2} - F_{\text{E}\text{O}_2}) / (1 - F_{\text{E}\text{O}_2}), \quad (1)$$

where  $\dot{V}$  is flow rate ( $\text{ml min}^{-1}$  at standard temperature and pressure) and  $F_{\text{I}\text{O}_2}$  and  $F_{\text{E}\text{O}_2}$  are incurrent and excurrent fractional  $\text{O}_2$  concentration, respectively. We used the lowest 1 min average within the last 5 min of a running interval to ensure that steady-state metabolism was reached. The coefficient of variation of  $\dot{V}_{\text{O}_2}$  data within the minimum 1 min periods did not differ between TH and non-TH groups, for either pre-enclosure or post-enclosure running trials (two-tailed *t*-tests;  $P=0.302$  and  $0.243$ , respectively). Mean mass-specific oxygen consumption per unit distance ( $\text{ml O}_2 \text{ g}^{-1} \text{ km}^{-1}$ ) was calculated using the mean of  $\dot{V}_{\text{O}_2}$  values from each of the  $16$ ,  $20$  and  $24 \text{ m min}^{-1}$  running intervals. Trial quality was assessed using a subjective scale (Swallow et al., 1998): ‘poor’ trials when mice failed to run, ‘fair’ trials when mice changed running direction or jumped around the treadmill, or ‘good’ trials when mice ran steadily and continuously in the same position on the treadmill. Only mice scoring ‘good’ at all running speeds for all of the pre-enclosure running trials were included in the study. Because of this, six male mice were excluded and replaced. For post-enclosure trials, all individuals obtained ‘good’ scores for running trials. All treadmill measurements and analyses were blind with respect to TH status and were completed by one individual (J.S.M.).

### Statistical analysis

To assess the influence of TH status, running speed and body mass on  $\dot{V}_{\text{O}_2}$ , a series of linear mixed-effects models (LMMs) were

conducted. First, a ‘full model’ was constructed predicting  $\dot{V}_{\text{O}_2}$  based on the fixed effects of TH status, body mass, running speed, time point (pre- versus post-enclosure) and all possible interactions; additionally, this model included the random effects of individual (as a slope with running speed) and population. Then a ‘best model’ was selected based on AICc scores from all possible candidates constructed by removing interaction terms and the fixed effect of time point. All candidate models included TH status (to directly test our hypothesis) and both body mass and running speed (as both have been strongly linked to oxygen consumption; Taylor et al., 1970, 1982). These models were based on 180 observations (three running speeds each, for both pre- and post-enclosure running trials) from 30 mice that form the three study populations. The model intercept for these models was set at non-TH males, mean mass ( $23.59 \text{ g}$ ), mean speed ( $20 \text{ m min}^{-1}$ ) and pre-enclosure. Models were remarkably consistent, indicating that no interaction was significant in any given candidate.

An additional series of LMMs was used to predict the mean mass-specific oxygen consumption per unit distance ( $\text{ml O}_2 \text{ g}^{-1} \text{ km}^{-1}$ ). This was calculated using the mean of  $\dot{V}_{\text{O}_2}$  values from the three running speeds. First, a ‘full model’ was constructed predicting mean mass-specific oxygen consumption per unit distance based on the fixed effects of TH status, body mass, time point and all possible interactions; additionally, this model included the random effects of individual and population. Then a ‘best model’ was selected based on AICc scores from all possible candidates constructed by removing interaction terms and the fixed effect of time point. All candidate models included TH status and body mass. These models were based on 60 observations (one each for both pre- and post-enclosure running trials) from 30 individuals and the intercept was set at non-TH males, mean mass ( $23.59 \text{ g}$ ) and pre-enclosure. Models were consistent in indicating that no interaction term was significant in any candidate.

Finally, to explicitly test for a difference in body mass between TH and non-TH males, we ran a LMM in which body mass was predicted by the fixed effects of TH status, time point and a TH status  $\times$  time point interaction. Individual and population were modeled as random effects. The model was based on 60 observations (one each for both pre- and post-enclosure mass measurements) from 30 individuals and the intercept was set for non-TH males and pre-enclosure. All LMMs were performed using the lmer function of the lme4 package (<http://cran.r-project.org/package=lme4>) in R (<http://www.R-project.org/>). Degrees of freedom and resulting *P*-values were calculated with a Satterthwaite approximation using the lmerTest package (<http://cran.r-project.org/package=lmerTest>). AICc scores were calculated using the AICcmodavg package (<http://cran.r-project.org/package=AICcmodavg>).

### RESULTS

Out of 30 male mice in the study, 11 held exclusive territories with a minimum of two females for at least 3 continuous weeks (TH;  $n=3$ , 4 and 4 for populations 1, 2 and 3, respectively). TH males successfully controlled exclusive territories for an average of 48 days out of 56 total days in the enclosures (the first week in enclosures is highly variable; following this, social patterns stabilize). The remaining 19 males were those that never successfully controlled a territory (non-TH).

Both the full and best models assessing the influence of TH status on  $\dot{V}_{\text{O}_2}$  indicate that TH males had higher  $\dot{V}_{\text{O}_2}$  than non-TH males (Table 1). Specifically, according to the full model, TH males had  $\dot{V}_{\text{O}_2}$  levels  $0.159 \pm 0.067 \text{ ml O}_2 \text{ min}^{-1}$  (mean  $\pm$  s.e.m.) higher than

**Table 1. LMM results for the influence of territory-holding (TH) status, body mass ( $M_b$ ), running speed and time point on oxygen consumption ( $\dot{V}_{O_2}$ )**

	Variance	s.d.	Estimate	s.e.m.	d.f.	t-value	Pr(> t )
<b><math>\dot{V}_{O_2}</math> full model</b>							
Random effects							
Individual×speed (slope)	0.0000	0.0007					
Population	0.0040	0.0632					
Fixed effects							
Intercept			2.624	0.054	3.6	48.22	<0.001***
TH status			0.159	0.067	35.4	2.38	0.023*
$M_b$			0.059	0.015	108.8	4.06	<0.001***
Speed			0.009	0.007	151.7	1.21	0.228
Time			0.018	0.032	134.8	0.56	0.578
TH status× $M_b$			-0.006	0.036	159.7	-0.16	0.871
TH status×speed			0.008	0.012	151.7	0.70	0.483
$M_b$ ×speed			-0.001	0.003	142.0	-0.24	0.807
TH status×time			-0.001	0.053	135.5	-0.01	0.991
$M_b$ ×time			0.004	0.012	152.9	0.33	0.741
Speed×time			0.006	0.010	134.5	0.63	0.530
TH status× $M_b$ ×speed			0.002	0.008	137.5	0.19	0.849
TH status× $M_b$ ×time			0.025	0.037	158.2	0.67	0.505
TH status×speed×time			0.006	0.016	134.5	0.37	0.712
$M_b$ ×speed×time			-0.001	0.004	135.8	-0.18	0.857
TH status× $M_b$ ×speed×time			0.006	0.009	136.6	0.64	0.524
<b><math>\dot{V}_{O_2}</math> best model</b>							
Random effects							
Individual×speed (slope)	0.0000	0.0007					
Population	0.0040	0.0596					
Fixed effects							
Intercept			2.639	0.049	3.0	53.53	<0.001***
TH status			0.136	0.057	35.1	2.40	0.022*
$M_b$			0.066	0.008	118.8	8.16	<0.001***
Speed			0.015	0.004	172.9	3.76	<0.001***

$\dot{V}_{O_2}$  (ml O<sub>2</sub> min<sup>-1</sup>) full model: linear mixed model (LMM) with 180 observations of 30 individuals in three populations. Intercept set at non-TH, mean  $M_b$  (23.59 g), mean speed (20 m min<sup>-1</sup>) and pre-enclosure levels.

$\dot{V}_{O_2}$  (ml O<sub>2</sub> min<sup>-1</sup>) best model: LMM with 180 observations of 30 individuals in three populations. Intercept set at non-TH, mean  $M_b$  (23.59 g) and mean speed (20 m min<sup>-1</sup>).

\* $P$ <0.05, \*\*\* $P$ <0.001.

those of non-TH males (LMM;  $t$ =2.38, d.f.=35.4,  $P$ =0.023).  $\dot{V}_{O_2}$  was also found to have a positive relationship with body mass, increasing by 0.059±0.015 ml O<sub>2</sub> min<sup>-1</sup> per gram (LMM;  $t$ =4.06, d.f.=108.8,  $P$ <0.001). Interactions between TH status and body mass or running speed did not significantly influence  $\dot{V}_{O_2}$  (LMM;  $P$ =0.871 and 0.483, respectively). Likewise, no significant interaction between TH status and time point was detected, indicating that the elevated  $\dot{V}_{O_2}$  of TH males did not change across the study (LMM;  $P$ =0.712). Similarly, the best-fitting model ( $\Delta$ AICc=2.31, relative to the next best candidate model) indicates that TH males had higher  $\dot{V}_{O_2}$  than non-TH males. TH males had  $\dot{V}_{O_2}$  levels 0.136±0.057 ml O<sub>2</sub> min<sup>-1</sup> higher than those of non-TH males (LMM;  $t$ =2.40, d.f.=35.1,  $P$ =0.022).  $\dot{V}_{O_2}$  was again found to have a positive relationship with body mass, increasing by 0.066±0.008 ml O<sub>2</sub> min<sup>-1</sup> per gram (LMM;  $t$ =8.16, d.f.=118.8,  $P$ <0.001). Additionally, running speed positively influenced  $\dot{V}_{O_2}$ , with levels increasing by 0.015±0.004 ml O<sub>2</sub> min<sup>-1</sup> per m min<sup>-1</sup> (LMM;  $t$ =3.76, d.f.=172.9,  $P$ <0.001). No interactions were included in this model nor was the fixed effect of time point.

TH status was also found to influence mean mass-specific oxygen consumption per unit distance according to both the full and best models (Table 2). Specifically, the full model indicates that TH males consumed 0.490±0.234 ml O<sub>2</sub> g<sup>-1</sup> km<sup>-1</sup> more than did non-TH males (LMM;  $t$ =2.09, d.f.=46.8,  $P$ =0.042; Fig. 1) and that there was a marginally statistically significant negative correlation with body mass (-0.113±0.059 ml O<sub>2</sub> g<sup>-1</sup> km<sup>-1</sup> per gram; LMM;  $t$ =-1.91, d.f.=52.0,  $P$ =0.062; Fig. 2); there was no interaction between

TH status and body mass ( $P$ =0.778). Moreover, mean mass-specific oxygen consumption per unit distance was not influenced by time point (LMM;  $P$ =0.596) nor was there a significant interaction between time point and TH status (LMM;  $P$ =0.943) or time point and body mass (LMM;  $P$ =0.920). The simplified best-fitting model ( $\Delta$ AICc=4.42, relative to the next best candidate model) indicates that TH males consumed 0.478±0.186 ml O<sub>2</sub> g<sup>-1</sup> km<sup>-1</sup> more than did non-TH males (LMM;  $t$ =2.58, d.f.=26.1,  $P$ =0.016) and that there was a statistically significant negative correlation with body mass (-0.117±0.032 ml O<sub>2</sub> g<sup>-1</sup> km<sup>-1</sup> per gram; LMM;  $t$ =-3.65, d.f.=47.8,  $P$ =0.001). No interactions were included in this model nor was the fixed effect of time point.

TH status did not influence body mass (Table S1). No significant difference in the body mass of TH and non-TH males was detected (LMM;  $P$ =0.810; Fig. S2). Body mass did not change between time points (LMM;  $P$ =0.902) nor was there a significant interaction with TH status (LMM;  $P$ =0.717).

## DISCUSSION

Our results show that TH male house mice have higher absolute  $\dot{V}_{O_2}$  as well as higher mean mass-specific oxygen consumption per unit distance (ml O<sub>2</sub> g<sup>-1</sup> km<sup>-1</sup>) when running at intermediate speeds (i.e. reduced locomotor economy) as compared with non-TH males. This difference was present both before and after 8 week competition trials in semi-natural enclosures. Prior to beginning the experimental protocol, all mice were individually housed in cages, indicating that this disparity is not a result of the experience of being

**Table 2. LMM results for the influence of territory-holding (TH) status, body mass ( $M_b$ ) and time point on mean distance-specific oxygen consumption ( $\text{ml O}_2 \text{g}^{-1} \text{km}^{-1}$ )**

	Variance	s.d.	Estimate	s.e.m.	d.f.	t-value	Pr(> t )
<b>Mean mass-specific oxygen consumption per unit distance full model</b>							
Random effects							
Individual	0.1037	0.3220					
Population	0.0015	0.0386					
Fixed effects							
Intercept			8.018	0.144	9.7	55.8	<0.001***
TH status			0.490	0.234	46.8	2.1	0.042*
$M_b$			-0.113	0.059	52.0	-1.9	0.062
Time			0.092	0.171	24.5	0.5	0.596
TH status $\times M_b$			0.046	0.163	48.4	0.3	0.778
TH status $\times$ time			-0.021	0.285	24.8	-0.1	0.943
$M_b \times$ time			-0.007	0.065	30.8	-0.1	0.920
TH status $\times M_b \times$ time			-0.043	0.182	41.1	-0.2	0.813
<b>Mean mass-specific oxygen consumption per unit distance best model</b>							
Random effects							
Individual	0.1193	0.3453					
Population	0.0020	0.0443					
Fixed effects							
Intercept			8.065	0.115	4.5	70.1	<0.001***
TH status			0.478	0.186	26.1	2.6	0.016*
$M_b$			-0.117	0.032	47.8	-3.7	0.001***

Mean mass-specific oxygen consumption per unit distance ( $\text{ml O}_2 \text{g}^{-1} \text{km}^{-1}$ ) full model: LMM with 60 observations of 30 individuals in three populations. Intercept set at non-TH, mean  $M_b$  (23.59 g) and pre-enclosure levels.

Mean mass-specific oxygen consumption per unit distance ( $\text{ml O}_2 \text{g}^{-1} \text{km}^{-1}$ ) best model: LMM with 60 observations of 30 individuals in three populations. Intercept set at non-TH and mean  $M_b$  (23.59 g) levels.

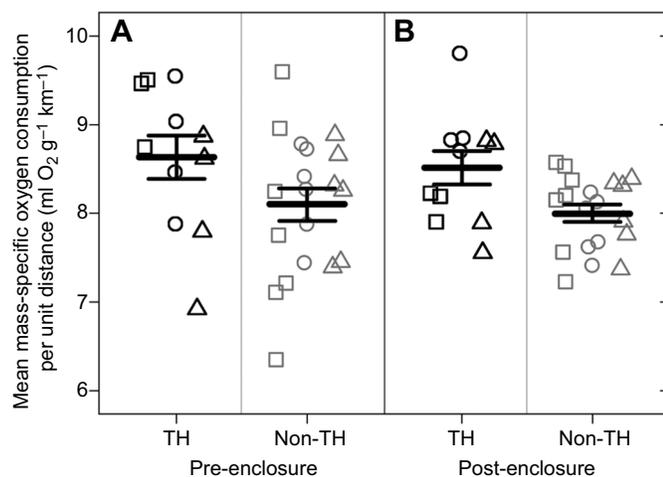
\* $P < 0.05$ , \*\*\* $P < 0.001$ .

in the competition enclosures (e.g. from stress, unequal access to food or water, injury, exhaustion or temporary hormone surges).

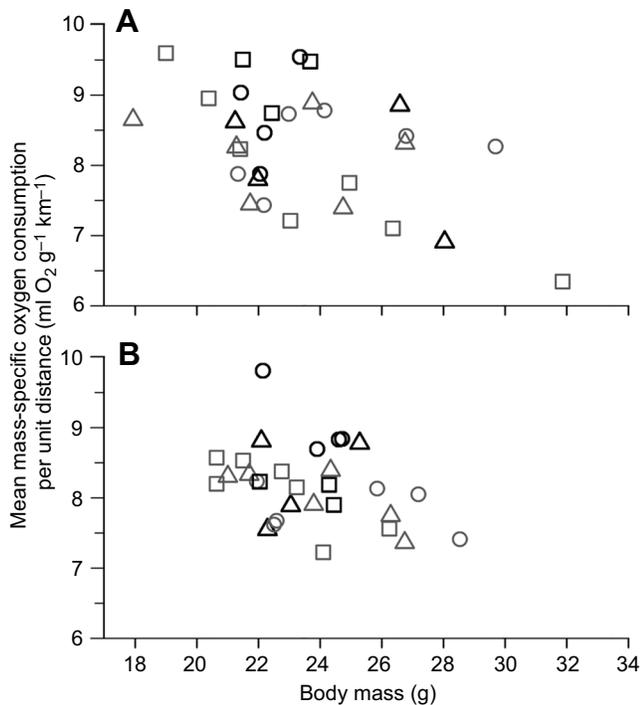
Analysis of oxygen consumption data indicated that, consistent with previous studies,  $\dot{V}_{\text{O}_2}$  increases with both running speed and body mass, and mean mass-specific oxygen consumption per unit distance decreases with body mass (Taylor et al., 1970, 1982). According to the model based on  $\dot{V}_{\text{O}_2}$ , the added energetic cost of running in TH males is metabolically equivalent to being 2.1 g

heavier or running 9.1  $\text{m min}^{-1}$  faster. The model based on mean mass-specific oxygen consumption per unit distance indicated that TH males expend 6.1% more energy to travel a given distance when running at intermediate running speeds. Assuming a resting metabolic rate of  $0.557 \text{ ml O}_2 \text{ min}^{-1}$  (based on a mean mass of 23.59 g from this study and the equation for resting metabolic rate from Rezende et al., 2009), this difference would result in a daily energetic saving substantial enough to sustain an individual at resting metabolic rate for about 37 min for each km traveled per day. If extrapolated to the average voluntary running distance of male lab mice provided with a running wheel (4.4  $\text{km day}^{-1}$ ; Koteja et al., 1999), this would result in a difference of  $1.496 \text{ ml O}_2 \text{ g}^{-1}$ , enough to sustain resting metabolism for more than 2.5 h. Thus, while the percentage difference between oxygen consumption rates is relatively small, this difference may have a notable impact on daily energetic expenditure.

A caveat of the present study is that we do not have data on the non-active metabolic rates of individual mice. While we cannot exclude the possibility that systematic differences in non-active metabolic rates between TH and non-TH males may contribute to the differences in locomotor economy identified in our study, this scenario seems unlikely for several reasons. First, the difference in mean mass-specific oxygen consumption between TH and non-TH males was  $0.398 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$  (calculated from effect of TH status in the best model for mean mass-specific oxygen consumption per unit distance). This represents 30% of the calculated mass-specific resting metabolic rate ( $1.418 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ , based on the equation of Rezende et al., 2009) and is close to or greater than 2 s.d. of mean basal metabolic rate from previous studies of lab mice (2 s.d. = 0.332 and  $0.458 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ; Konarzewski and Diamond, 1995; Wone et al., 2009). Thus, a difference of this magnitude in non-active metabolic rates between TH and non-TH males seems unlikely. Second, a previous study on another rodent species (bank voles, *Myodes glareolus*) found no association between male social dominance in competitive arenas and basal metabolic rate (Radwan et al., 2004).



**Fig. 1. Mean mass-specific oxygen consumption per unit distance across intermediate running speeds for territory-holding (TH) and non-TH male house mice.** Data are from running trials before (A) and after (B) competition trials in semi-natural enclosures. Populations are represented by unique symbols; black symbols indicate TH males and gray symbols indicate non-TH males. Scatter was added to horizontal values to aid visualization. Means  $\pm$  s.e.m. are shown by bars. TH males had 6.1% greater mean mass-specific oxygen consumption rates than non-TH males (LMM;  $P < 0.05$ ).



**Fig. 2. Relationship between mean mass-specific oxygen consumption per unit distance and body mass for TH and non-TH male house mice.** Data are for running trials and body masses before (A) and after (B) competition trials in semi-natural enclosures. Populations are represented by unique symbols; black symbols indicate TH males and gray symbols indicate non-TH males. According to the best-fitting model, mean mass-specific oxygen consumption per unit distance decreased with body mass (LMM;  $P < 0.05$ ).

Interestingly, body mass was not correlated with territory control in our study, either before or after competition trials. Variance in post-enclosure body mass was greater among non-TH than among TH males (Bartlett test;  $P = 0.031$ ). These data suggest that an intermediate body mass may be optimal for securing and maintaining exclusive territories, possibly because of the importance of agility and maneuverability in the dynamic actions of physical fighting (*sensu* Székely et al., 2000; Lailvaux et al., 2004; Lawler et al., 2005; Lailvaux and Irshick, 2006; Raihani et al., 2006; Lawler, 2009). Indeed, recent evidence from the same experimental system used in the present study indicates that males of intermediate body mass have greater reproductive fitness than larger or smaller males (Ruff et al., 2017).

While territory control equates to greater reproductive fitness in this study system (based on genetic parentage analysis; Carroll et al., 2004) and others (Andersson, 1994), higher locomotor costs in TH males may impose viability costs in the manner of increased foraging time to meet their higher energetic demands. This would effectively decrease free energy and time for other activities and may increase mortality risk by exposing individuals to a greater threat of predation (Blanckenhorn, 2000). Sexually selected behaviors (i.e. fighting for territory and mates, and scent marking) are also energetically costly (Karasov, 1992; Briffa and Sneddon, 2007). When combined with the high energetic costs of locomotion (26–28% of total daily energetic expenditure in laboratory mice; Rezende et al., 2009), this may lead to phenotypic or behavioral constraints, and ultimately fitness costs, via resource allocation trade-offs (Zera and Harshman, 2001; Lailvaux and Husak, 2014). Alternatively, TH males may avoid these potential viability costs

through the decreased foraging time/distance allowed by living in high-quality resource-rich territories. However, males that are not capable of controlling high-quality territories likely spend more time foraging because they are often in lower quality habitats and may spend more time dispersing and traveling while seeking out available territory. The lower locomotor costs that we found in non-TH males may be beneficial in these circumstances and may also be advantageous in variable resource environments, particularly when food is ephemeral and abundance is low. In natural environments (as compared with our semi-natural settings with food *ad libitum*), resource acquisition limitations may exacerbate performance constraints underlying trade-offs (Blanckenhorn, 2000; Lailvaux and Husak, 2014).

The performance differences identified in this study are likely caused by conflicting functional demands within the musculoskeletal system. Fighting between mice involves biting, pushing, grappling and lunging (Miczek et al., 2001). Mice in the present study exhibited these behaviors during frequent fighting and as indicated by characteristic wounding (J.S.M., personal observation). Many of these actions are accomplished using the same anatomical structures that comprise the primary locomotor system (i.e. limb bones and muscles). This creates a conflict because the demands imposed by economical locomotion and fighting predict optimization in opposing directions (i.e. long, gracile limbs versus stout, muscular limbs). Comparisons of closely related species, such as cheetahs and lions or gibbons and gorillas, exemplify these disparate phenotypes as well as the corresponding social behaviors (i.e. low to high levels of male–male competition) and mating systems (i.e. non-polygynous to highly polygynous) associated with each (Carrier, 2002). Within a species or sex, however, simultaneous specialization for both aggression and economical locomotion is not possible without the evolution of novel structures, behaviors or other mechanisms of compensation (Oufiero and Garland, 2007; Husak and Lailvaux, 2014). For example, the evolution of horns in bovids, antlers in cervids and bipedal hopping in kangaroos (by freeing the forelimbs) have allowed both a high degree of cursoriality and polygynous mating systems with intense male–male competition (Carrier, 2002). In these taxa, the constraints imposed by locomotion–aggression trade-offs have been circumvented by decoupling anatomical weapons from the primary locomotor system. The apparent lack of novel solutions in mice and other mammals may limit performance in functionally conflicting tasks.

In summary, we found that TH male house mice have reduced locomotor economy compared with non-TH males. These results are likely caused by a functional trade-off between economical locomotion and physical fighting (Carrier, 2002). Locomotor economy is an important performance trait because it is a major determinant of total daily energetic expenditure, and therefore is relevant to many vertebrate species. Additionally, we directly measured territory control, which, in our study system, is a proxy for reproductive success. These methods allowed direct comparison of two whole-organism performance traits that are important components of Darwinian fitness. We suggest that future studies on performance disparities may be improved by incorporating an energetics-based approach to the examination of locomotor traits that may be in functional conflict with sexually selected performance traits.

#### Acknowledgements

We thank L. Morrison for colony management and data collection; D. Cornwall for assistance with animal processing; C. Farmer for respirometry equipment

and instruction; and M. Chappell, B. Cieri and A. Cooper for useful discussions. P. Koteja and one anonymous reviewer provided feedback that greatly improved the manuscript.

#### Competing interests

The authors declare no competing or financial interests.

#### Author contributions

Conceptualization: J.S.M.; Methodology: J.S.M., J.S.R., W.K.P., D.R.C.; Formal analysis: J.S.M., J.S.R.; Investigation: J.S.M.; Data curation: J.S.M.; Writing - original draft: J.S.M.; Writing - review & editing: J.S.R., W.K.P., D.R.C.; Visualization: J.S.M.; Funding acquisition: J.S.M., W.K.P., D.R.C.

#### Funding

This work was supported by the US National Institutes of Health (grant R01-GM109500 to W.K.P.) and US National Science Foundation (grant IOS-0817782 to D.R.C.; grant DDIG DEB-1600727 to J.S.M.). Deposited in PMC for release after 12 months.

#### Data availability

Data are available from the Dryad Digital Repository (Morris et al., 2017): <http://dx.doi.org/10.5061/dryad.p11b0>.

#### Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.154823.supplemental>

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