

Original Article

Costs of elaborate weapons in a rhinoceros beetle: how difficult is it to fly with a big horn?

Erin L. McCullough, Paul R. Weingarden, and Douglas J. Emlen

Division of Biological Sciences, University of Montana, 32 Campus Drive, HS 104, Missoula, MT 59812, USA

The giant horns of rhinoceros beetles exemplify the extreme morphologies that can result from sexual selection. Ornaments and weapons help males obtain mates but may also impose fitness costs. Intuitively, exaggerated sexually selected traits should impair locomotion, yet compensatory morphologies often make it difficult to detect locomotor costs. Here, we tested whether horns of the rhinoceros beetle *Trypoxylus dichotomus* impair flight and whether males compensate by developing larger wings or flight muscles. Contrary to our expectation that horns are costly for flight, males flew as fast as females, and among males, horn length was not correlated with flight speed or distance flown. We found some evidence for compensations in the male flight apparatus; males had relatively larger wings and flight muscles than females, and males with long horns for their body size had larger wings than males with relatively short horns. Flight muscle mass, however, was unaffected by horn length. We conclude that *T. dichotomus* horns may have been costly in the past and led to morphological compensations in wing and flight muscle size, but they do not currently impose significant flight costs. Fitness costs are a central tenet of sexual selection theory, and the large horns of rhinoceros beetles are expected to impose particularly strong costs on locomotion. Given our finding that *T. dichotomus* horns are surprisingly easy to carry, future work will be needed to identify the potential costs that have been important in shaping the evolution of elaborate horn morphologies. *Key words*: compensations, costs, flight, horns, rhinoceros beetles, sexual selection. [*Behav Ecol*]

INTRODUCTION

Competition for mates is a potent driver in the evolution of animal morphology and has led to many of Nature's most impressive and beautiful forms: the massive antlers of elk, the elongated tail feathers of birds, and the colorful dewlaps of lizards (Darwin 1871; Andersson 1994). Although sexually selected ornaments and weapons help males obtain mates, they may also come with fitness costs (Kirkpatrick 1982; Grafen 1990; Iwasa et al. 1991). Specifically, sexually selected traits may impair locomotion (Barbosa and Møller 1999; Moczek and Emlen 2000; Basolo and Alcaraz 2003; Madewell and Moczek 2006; Allen and Levinton 2007), increase risk of predation or parasitism (Møller and Nielsen 1997; Zuk and Kolluru 1998; Godin and McDonough 2003), weaken the immune system (Folstad and Karter 1992; Saino and Møller 1996; Verhulst et al. 1999; Rantala et al. 2003), or stunt the growth of other body structures (Kawano 1995, 1997, 2006; Emlen 2001). Importantly, the very reason why choosy females and rival males are expected to pay attention to ornaments and weapons is because they are costly, as traits that are difficult to produce and maintain are likely to be honest indicators of a male's quality (Zahavi 1975; Kodric-Brown and Brown 1984; Nur and Hasson 1984; Zeh and Zeh 1988; Grafen 1990; Searcy and Nowicki 2005).

Given the large size of many male ornaments and weapons, impaired locomotion may be a particularly important cost of bearing sexually selected traits (Oufiero and Garland 2007).

Yet empirical evidence for locomotor costs is equivocal. For example, the long tail ornaments of certain hummingbird species increase flight metabolic costs and reduce maximum flight speed. However, these costs are most evident only at high flight speeds, which are rare for flying hummingbirds. As a result, long tails probably impose a relatively minor increase in daily energetic costs (Clark and Dudley 2009). The elongated eyestalks of sexually dimorphic stalk-eyed flies also do not appear to impose substantial flight costs. Although long-eyed males ascended at shallower angles and slower velocities than short-eyed females, males and females did not differ in horizontal flight velocity, and males actually flew tighter turns and turned more frequently than females (Swallow et al. 2000; Ribak and Swallow 2007). Even the tails of barn swallows—a classic and well-studied example of an exaggerated sexually selected trait—may not be costly, as long tail feathers increase drag (Evans and Thomas 1992; Barbosa and Møller 1999) but also enhance maneuverability (Thomas 1993; Norberg 1994; Buchanan and Evans 2000). Thus, although the costs of male ornaments and weapons are central to sexual selection theory, strong empirical support for locomotor costs is lacking (Kotiaho 2001; Husak and Swallow 2011).

The costs of sexual traits may be difficult to detect because organisms evolve as integrated units. As a result, elaborated traits can become developmentally integrated with other traits that are not the primary targets of sexual selection but that enable individuals to use, display, or bear their sexually selected traits more effectively (Tomkins et al. 2005). In some cases, these correlated traits may offset the negative performance consequences of bearing sexually selected traits and thereby complicate the relationships between sexual trait size and locomotion (Møller 1996; Oufiero and Garland 2007; Husak and Swallow 2011). For example, in both long-tailed birds and stalk-eyed flies, males have proportionately longer wings

Address correspondence to E.L. McCullough. E-mail: erin.mccullough@umontana.edu.

Received 16 December 2011; revised 5 March 2012; accepted 23 March 2012.

than females, which may help them compensate for the aerodynamic costs of their sexual ornaments (Balmford et al. 1994; Ribak et al. 2009). These modifications presumably allow males to “have their cake and eat it too”: to display sexually selected traits without sustaining undue costs on locomotion. However, compensatory morphologies also make performance costs difficult to detect and may help explain why gender differences in performance, or functional tradeoffs between sexual traits and performance, oftentimes are not found (Ribak and Swallow 2007; Worthington and Swallow 2010). It is now clear that studies examining the potential costs of sexually selected traits must also consider the possibility for compensatory mechanisms because ignoring the consequences of these correlated traits may lead to erroneous conclusions about the costs of sexually selected traits (Oufiero and Garland 2007).

Rhinoceros beetles are an ideal system for examining the locomotor costs of a sexually selected trait due to the large size and elaborate architectures of their horns. For example, in the Japanese horned beetle *Trypoxylus dichotomus* (formerly known as *Allomyrina dichotoma*), males have a pitchfork-like horn that extends forward from the head, and horn length can be nearly two-thirds the length of the rest of the body (Figure 1). The benefit of having an exaggerated horn is clear: Males with longer horns are more likely to win fights against rival males and gain mating opportunities (Siva-Jothy 1987; Karino et al. 2005; Hongo 2007). However, little is known about the costs of bearing large horns in rhinoceros beetles (but see Hongo 2010), despite their important implications for potential evolutionary, developmental, and physiological constraints on weapon size and form.

Here, we examine the costs of beetle horns by comparing flight speeds and distances flown by free-flying male and female *T. dichotomus*. Intuitively, the large branched head horn should impair a male's ability to fly. We therefore predict that horned males will fly slower and shorter distances than hornless females and that among males, horn size will tradeoff with flight performance. However, even if horns impair locomotion, males and females may fly equally well if males have evolved compensatory adaptations in their flight apparatus. We therefore compared investment in wing size and flight muscle to examine if and to what degree males minimize the net cost of their giant horns.

MATERIALS AND METHODS

Trypoxylus dichotomus is a large rhinoceros beetle common throughout mountainous regions in East Asia. The species exhibits a wide variation in both body size and horn size. Large males have a long branched head horn and sharp thoracic horn; small males have a short head horn and tiny thoracic horn; and females have no horns at all.



Figure 1
Large male *Trypoxylus dichotomus* showing the long branched head horn and sharp thoracic horn.

Flight performance

Field experiments were conducted on the National Chi Nan University campus in central Taiwan. The campus grounds contain many (>120) *Fraxinus* trees, which is the exclusive host plant of *T. dichotomus* in Taiwan. Beetles chew into the bark and feed on the exuding sap. The study was conducted in June and July when adults are abundant and most active. Beetles were collected from their natural sap sites and individually marked with quick drying paint markers. Each beetle was given a unique color combination on its elytra and number on its prothorax for identification. Horn length of all males and body size (measured as prothorax width) of both males and females were measured to the nearest 0.01 mm with dial calipers (Mitutoyo, Japan). (For justification for using thoracic width as a measure of body size, see Emlen 1997.) All beetles were released to their original feeding trees after being marked and measured.

We examined 2 measures of the beetles' flight performance: speed and distance. Flight speed was measured directly on free-flying beetles to the nearest 0.1 km/h using a high performance speed sensor (Stalker ATS Performance Radar Gun, Plano, TX). Beetles were observed taking off from the ground on their own accord, and flight speed was recorded once the beetle reached a stable cruising speed flying directly away from the observer. To control for effects of ambient wind, flight speeds were only measured on clear windless nights. We measured flight speeds of 137 males and 74 females. Flight speeds were averaged in cases where an individual was measured more than once (males: $n = 48$; females: $n = 7$).

To measure flight distances, we scanned all feeding trees within the study site every night and recorded the locations of any marked beetles. Distances between trees were measured to the nearest 1 m with a global positioning system (Garmin GPSMAP 60CSx, Olathe, KS). To verify that our scan samples were an accurate measure of the beetles' flight distances, we equipped a subset of marked beetles (males: $n = 15$; females: $n = 6$) with radio transmitters to measure flight distances directly. The small 0.2 g radio transmitters (Advanced Telemetry Systems, Series A2405, Isanti, MN) did not appear to affect the beetles' flight performance or behavior. Flight speeds did not differ between beetles with radios (2.21 ± 0.33 m/s) to the same beetles without radios (2.16 ± 0.39 m/s; $T = -0.28$, degrees of freedom [df] = 14, $P = 0.78$), and radio-tagged beetles appeared to feed and mate normally.

Radiotelemetry revealed that beetles usually hide during the daytime in the canopy of their feeding tree or a neighboring nonhost tree or sometimes will bury themselves in the grass, leaf litter, or dirt near their feeding tree. A few radio-tagged males were occasionally found hiding in a nonhost tree up to 400 m from their nighttime feeding site. Because these trips to nonhost trees could not be detected by scanning the feeding trees, our scan samples may have underestimated some beetle movements. However, these hiding trees were all located within the study site, and the distances to and from these nonhost trees were well within the range of flight distances observed among feeding trees. We are therefore confident that the nightly scan samples represent an accurate measure of the typical distances flown by the beetles in our study.

We recorded flight distances of 399 males and 28 females. Because the sample size for female distances was so small, and because we suspect that our scan samples may significantly underestimate female flight distances, we did not test for a sex difference in flight distances. Unfortunately, because we were only able to track a small number of females via scan sampling and radiotelemetry, we do not yet know how far females typically travel. The maximum flight path recorded for each individual was used in our statistical analyses.

Compensatory traits

We examined beetles for 2 potential compensatory traits: increased wing size and increased flight musculature. The beetles used in these morphological measurements were purchased as final instar larvae from a commercial insect distributor (Yasaka Kabuto Kuwagata World, Hamada City, Japan) and reared to adulthood in our laboratory at the University of Montana. Horn length of all males and prothorax width of both males and females were measured to the nearest 0.01 mm with dial calipers (Mitutoyo, Japan). Body mass of all beetles was measured to the nearest 0.001 g with an analytical balance (Mettler Toledo, Columbus, OH). After being measured and weighed, the beetles were placed in airtight containers and euthanized by freezing.

To measure wing size, we severed both left and right hind wings from the thorax at the base of the wing hinge and pressed the wings between 2 glass plates. We took digital photographs of the wings and imported the images into imaging software (ImageJ v1.41, National Institutes of Health, Bethesda, MD) for calibration and analysis. Wing length was measured as the distance between the base of the wing hinge to the most distal point on the curved wing tip. Wing area was measured as the area inside a manually traced outline of each wing.

To measure flight musculature, we isolated the pterothorax (hereafter referred to simply as the thorax) from each frozen specimen and cut it in half sagittally. Any visible esophageal contents and nonmuscle tissues were removed, and both halves were weighed immediately. The procedure took less than 2 min, and there was no measurable water loss over this time period. The thorax was then soaked in 1 M NaOH for 24 h, rinsed with water to remove all dissolved muscle tissue, dried at room temperature for 24 h, and reweighed. Flight muscle mass was found by subtracting the empty exoskeleton mass from the original thoracic mass (Marden 1987).

Analysis of male dimorphism

Although previous studies have described *T. dichotomus* as male dimorphic (Iguchi 1998; Hongo 2003, 2007; Karino et al. 2005; Plaistow et al. 2005), there are no obvious behavioral differences between the 2 morphs. Both major males and minor males use their horns to pry rival males away from sap sites that attract females and both morphs exhibit sneaking behavior (Hongo 2003, 2007). Nevertheless, visual inspection of the relationship between male horn length and body size suggests that it is nonlinear. We therefore analyzed horn versus body size measures for possible nonlinear allometries (Knell 2009). To statistically test for the presence or absence of male dimorphism, we fitted the quadratic model: $y = \alpha_0 + \alpha_1 x + \alpha_2 x^2 + \varepsilon$, where y is the natural log of horn length, x is the natural log of body size (measured as prothorax width), α is a regression coefficient, and ε is the random error. The regression coefficient α_2 was significantly different from zero ($\alpha_2 = -2.33$, $T = -8.64$, $df = 980$, $P < 0.001$), and the quadratic model described the data significantly better than the simple linear model: $y = \alpha_0 + \alpha_1 x + \varepsilon$ ($F_{981,980} = 74.61$, $P < 0.001$). Further analyses were therefore performed to characterize the nonlinear relationship between horn length and body size.

Briefly, we compared 3 models on the basis of their goodness of fit (Akaike's information criterion, AIC) to determine which model best described the relationship between horn length and body size in our data: a switch-point model using the procedure outlined by Eberhard and Gutierrez (EG) (1991), a switch-point model using the Segmented package in R (Mugge 2003), and a quadratic model. The EG switch-point model fit the data significantly better than the other 2 models

(EG model AIC = 3631, segmented model AIC = 3643, quadratic model AIC = 3712). According to this model, the switch-point in body size that delineated major males from minor males was 23.41 mm, and the relationship between horn length and body size differed in both slope ($T = -5.79$, $P < 0.001$) and intercept ($T = 6.59$; $P < 0.001$) among major and minor males. Males with a pronotum width ≥ 23.41 mm were classified as major males and males with a pronotum width < 23.41 mm were classified as minor males.

Statistical analyses

We examined the effect of body size on the beetles' flight performance using ordinary least squares linear regressions. To test for the effect of horn size on male flight performance, we then fitted general linear models (GLMs) to the male data set with horn length, body size (measured as pronotum width), and morph as explanatory variables. Models were initially fitted with all second-order interactions included and simplified to the minimum adequate model by sequentially removing non-significant terms on the basis of deletion tests (Crawley 2007). We tested for a sex difference in flight speed using Student's t test.

The allometric relationships between body size and the potential compensatory traits (wing size and flight musculature) were examined using the power equation: $y = ax^b$, where x is body mass and y is wing length, wing area, or flight muscle mass. We log transformed all morphological variables before analyses. We assumed that wing size and flight musculature in females were near the naturally selected optima (Lande 1980) and tested for compensations by comparing the scaling exponents (b) and scaling factors (a) of the allometric relationships between males and females. Because horn length exhibits positive allometry (i.e., large males have disproportionately long horns), we expected large males to incur relatively higher flight costs than small males. If males compensate for the cost of bearing horns, and wing size and flight muscle mass is commensurate with the magnitude of these costs, we expected the scaling exponents (i.e., allometric slopes) for wing size and flight muscle mass to be greater for males than females. We conducted our analyses using standardized major axis (model II) regression with the SMATR package in R (Warton et al. 2006).

To further explore the effect of horn length on wing and flight muscle size, we fitted a GLM to the male data set with horn length, body mass, and morph as explanatory variables and all second-order interactions. The minimal adequate model was selected by deletion tests (Crawley 2007).

RESULTS

Flight performance

The elaborate horns of male *T. dichotomus* do not inhibit the beetles' flight performance, at least in terms of how fast or how far beetles fly. There was no correlation between flight speed and body size in either males ($R^2 = 0.002$, $F_{1,135} = 0.22$, $P = 0.64$) or females ($R^2 = 0.008$, $F_{1,72} = 0.54$, $P = 0.46$). Among males, flight speed was unaffected by horn length, body size, morph, or any interactions among these variables. Model simplification indicated that the minimum adequate model predicting male flight speed was the null model (Table 1). There was no difference in average flight speed between males and females ($T = 0.53$, $df = 127$, $P = 0.60$; Figure 2). All beetles flew between 1 and 4 m/s (mean = 2.27, standard deviation = 0.44).

Males were typically seen on repeated nights, in some cases for up to almost 2 months after their initial capture, and several males flew close to 1 km between feeding trees. Females, on

Table 1
Explanatory variables retained and removed (shown in *italics*) for the GLM predicting male flight speed

Explanatory variable	Coefficient	Standard error	F	P
Intercept	2.28	0.035		
<i>Horn length (HL)</i>			1.17	0.282
<i>Prothorax width (PW)</i>			2.66	0.106
<i>Morph</i>			0.305	0.582
<i>HL:PW</i>			2.86	0.093
<i>HL:Morph</i>			2.66	0.106
<i>PW:Morph</i>			0.279	0.598

The *F*-statistics and *P* values are from partial *F*-tests comparing the goodness of fit between models with and without the explanatory variable in question when less significant terms have been removed.

the other hand, were typically seen for only 1 or 2 days after their initial capture (if at all) and rarely moved far from the feeding tree on which they were first sighted. However, most of the radio-tagged females flew out of the detection range of our receiver (ca. 800 m, depending on terrain). These results suggest that females also fly long distances between feeding and oviposition sites and may even fly farther distances than males.

There was no correlation between flight distance and body size in either males ($R^2 = 0.008$, $F_{1,397} = 3.37$, $P = 0.07$, Figure 3) or females ($R^2 = 0.002$, $F_{1,26} = 0.04$, $P = 0.85$). Among males, distance flown was unaffected by horn length, body size, morph, or any interactions among these variables (Supplementary Table 1).

Compensatory traits

Our results suggest that male *T. dichotomus* compensate for their horns by investing relatively more in their flight apparatus. The scaling exponents (i.e., allometric slopes) did not differ between males and females for wing length (likelihood ratio test: $lr = 2.10$, $P = 0.15$), wing area ($lr = 0.60$, $P = 0.44$), or flight muscle mass ($lr = 0.006$, $P = 0.94$; Figure 4). However, the scaling factors (i.e., allometric intercepts) did differ significantly between males and females for all 3 flight-related morphologies. In all cases, the scaling factor was significantly

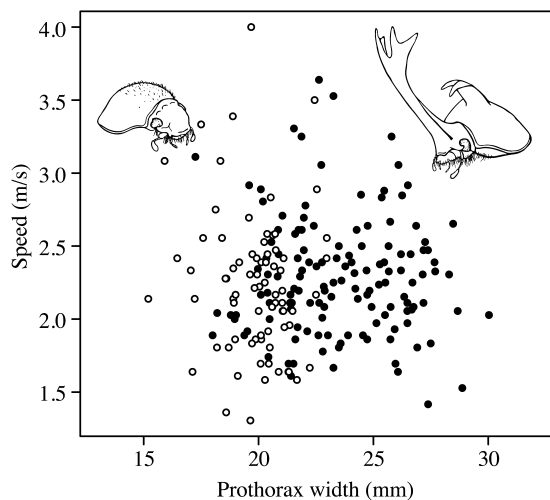


Figure 2
Relationships between prothorax width and flight speed for males (closed circles: $R^2 = 0.002$, $F_{1,135} = 0.22$, $P = 0.64$) and females (open circles: $R^2 = 0.008$, $F_{1,72} = 0.54$, $P = 0.46$).

higher for males than females (wing length: Wald test, $W = 42.7$, $P < 0.001$; wing area: $W = 39.9$, $P < 0.001$; flight muscle mass: $W = 34.8$, $P < 0.001$; Figure 4). Specifically, compared with females, males have a 4% mass-specific increase in wing length, a 10% increase in wing area, and a 7% increase in flight muscle mass.

When we examined patterns of morphological variation among males, body mass was the only significant predictor of flight muscle mass (Supplementary Table 2). In contrast, wing length (Table 2) and wing area (Supplementary Table 3) were affected by body mass, horn length, and morph. Males with long horns for their body size had longer and larger wings than males with relatively short horns and major males had slightly longer and larger wings than minor males, even after accounting for differences in horn and body size.

DISCUSSION

Sexually selected ornaments and weapons are assumed to be costly. *Trypoxylus dichotomus* offers an ideal system for measuring the locomotor costs of a male weapon. In this species, males must fly to and from sap sites every night to mate with females, yet males have a long branched head horn that presumably makes flying difficult. Contrary to our predictions, males flew as well as hornless females, and among males, there was no correlation between horn length and either flight speed or flight distance. We offer 3 possible explanations for these unexpected results. First, horns may be costly to beetles for other unmeasured aspects of locomotion. Second, horns may impair flight, but beetles offset these costs by producing larger wings and flight muscles. Third, the exaggerated horns of rhinoceros beetles simply may not be as costly for flight as we imagined.

The speed at which a beetle flies and the distance over which it typically travels are just two of the many proxies of beetle flight performance. Although we found no sex difference in flight speed and no tradeoffs between horn size and flight speed or distances flown, the horns of *T. dichotomus* may affect other aspects of flight performance (e.g., takeoff ability, horizontal or vertical acceleration, maneuverability) that were not measured in this study. Alternatively, horns may affect the beetles' terrestrial locomotion. In dung beetles, for example, long horns reduce running speed and maneuverability inside underground tunnels (Moczek and Emlen 2000; Madewell and Moczek 2006), and the long horns of *T. dichotomus* may

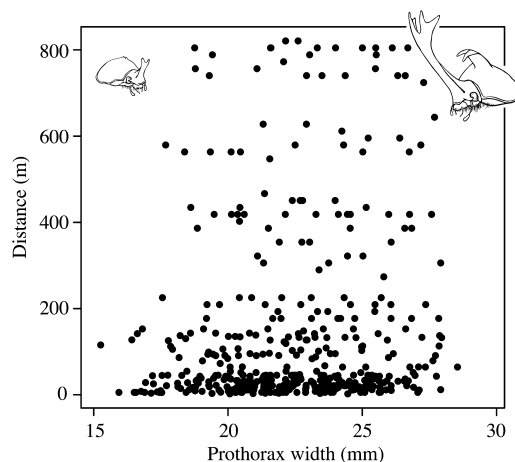


Figure 3
Relationship between prothorax width and distance flown for males ($R^2 = 0.008$, $F_{1,397} = 3.37$, $P = 0.07$).

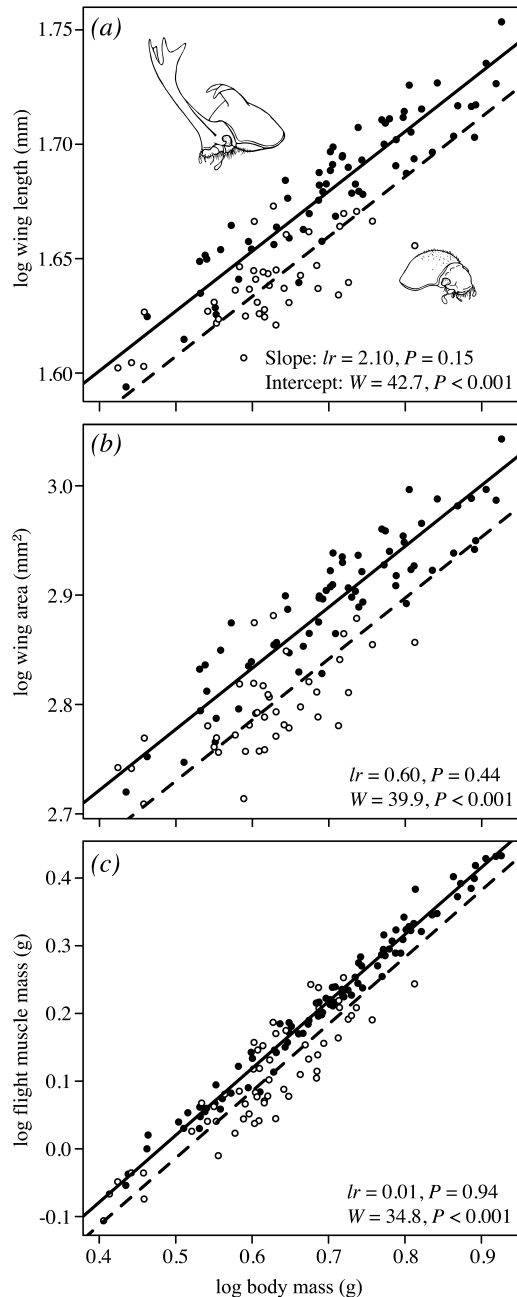


Figure 4
Allometric relationships between body mass and (a) wing length, (b) wing area, and (c) flight muscle mass. Males = closed circles, females = open circles. Lines represent the standardized major axis regression lines for males (solid lines) and females (dashed lines).

similarly impair the males' ability to maneuver around sap sites on the trunks and branches of trees. Nevertheless, flying (rather than walking) is the primary mode of locomotion for *T. dichotomus*, so flight speed and distances flown are likely to be the most ecologically relevant measures of performance for this species. Whether or not a male rhinoceros beetle mates depends on his ability to protect resource sites that attract females. In *T. dichotomus*, males guard wounds on the sides of trees where females come to feed (Hongo 2007). A male's reproductive success therefore depends on his ability to find and fly to sap sites, to return to a sap site if he is kicked off it by a rival male, and to travel to new sap sites and mate

Table 2

Explanatory variables retained and removed (shown in *italics*) for the GLM predicting male wing length

Explanatory variable	Coefficient	Standard error	<i>F</i>	<i>P</i>
Intercept	2.28	0.05		
Log(Mass)	0.218	0.048	302.33	<0.001
Log(HL)	0.349	0.056	40.75	<0.001
Morph	0.017	0.008	5.23	0.026
<i>Log(Mass):Log(HL)</i>			1.79	0.186
<i>Log(Mass):Morph</i>			1.09	0.301
<i>Log(HL):Morph</i>			0.936	0.337

The *F*-statistics and *P* values are from partial *F*-tests comparing the goodness of fit between models with and without the explanatory variable in question when less significant terms have been removed. HL, horn length.

with additional females. Furthermore, flight speed is likely to directly affect a beetle's ability to evade aerial predators (Hongo and Kaneda 2009). As a result, flight speed and distances flown may represent the aspects of performance that have the most direct effects on a beetle's fitness. We were unable to measure male reproductive success in this study, however, so future work is warranted to assess the actual fitness consequences of variation in locomotor performance.

A second explanation is that males compensate for the cost of large horns by investing more in their flight apparatus. We tested this hypothesis in 2 ways: by comparing wing and flight muscle allometries between horned males, and hornless females and by examining among-male variation in wings and flight musculature after accounting for differences in body size. We found evidence for partial but not perfect compensation from both of these analyses. Specifically, we found that the scaling factors for wing size and flight muscle mass were significantly higher for males than females. At any given body size, males had significantly larger wings and flight muscles than females. However, males did not have steeper allometries than females. Thus, large males did not have disproportionately large wings or flight muscles, as we would expect if they fully compensated for their disproportionately long horns. Additionally, among males, we found that horn length significantly affected wing length and wing area, even after controlling for variation in body size. In contrast, there was no effect of horns on flight muscle mass. As a result, males with long horns for their body size compensate by developing longer and larger wings but do not adjust the size of their flight muscles. Future studies, however, should examine whether mitochondrial density, tracheal density, or other aspects of flight muscle physiology vary between males and females or between major and minor morphs.

A third explanation for why males and females do not differ in their ability to fly is that horns simply are not that costly. That is, if horns do not make flying generally more difficult, then males and females would not be expected to differ in flight performance. We find this hypothesis counterintuitive, especially given the striking size of horns in *T. dichotomus* and other rhinoceros beetle species. Nevertheless, the fact that males and females fly equally well and that males are preyed upon less frequently than females (Hongo and Kaneda 2009) suggest that horns are not especially costly to carry. In fact, in a similar study comparing the flight ability of *T. dichotomus* males, Hongo (2010) found that larger males flew slightly faster than smaller males, which is the opposite trend of what would be expected if horns impeded flight.

It is important to note, however, that even if horns are not costly to carry in present-day beetles, the fact that males invest

more in their flight apparatus by producing relatively larger flight muscles and wings suggests that horns were costly to flight in the past. For example, in many long-tailed bird species, there is a positive relationship between male wing size and tail length, which probably reflects selective pressure to overcome the added drag of the male tail ornaments (Evans and Thomas 1992; Andersson and Andersson 1994; Balmford et al. 1994; Møller et al. 1995). Similarly in stalk-eyed flies, the positive correlation between sexual dimorphism in wing length and eye-span most likely reflects selection to offset the increased rotational inertia imposed by long eye-spans, as longer wings allow males to generate stronger torques per wing beat (Swallow et al. 2000; Ribak et al. 2009). If long tails did not increase drag or if long eye-spans did not reduce maneuverability, we would not expect birds and flies to evolve compensatory increases in male wing size. We intuitively expect compensatory changes to imply costs. Thus, the simple observation that *T. dichotomus* males have relatively larger flight muscles and wings than females suggests that the locomotor costs of horns were once strong enough to act as agents of selection on the beetles' flight apparatus. We suggest that horns historically imposed substantial flight costs and led to compensations in wing and flight muscle size but that these costs have been mitigated in present-day beetles. Similar to the narrowed tips of ornamental tail feathers in male birds that have evolved to minimize aerodynamic drag (Møller and Hedenström 1999), we suggest that the structure and composition of the horn itself has become modified over time to significantly reduce horn mass and minimize flight costs (McCullough EL and Tobalske BW, in preparation).

We recognize at least 2 potentially important limitations to this study. First, we compared wing size and flight muscle mass between males and females in order to test whether males compensate for the costs of bearing horns. Female *T. dichotomus* are hornless, so they are a convenient natural control for examining the effects of horns on the beetles' flight apparatus. However, these comparisons may be misleading because females certainly are not males that simply lack horns. In particular, males and females may differ substantially in their reproductive investments (e.g., Stearns 1992), so females may deviate from the naturally selected optima in wing size and flight musculature due to their own resource allocation constraints. As a result, any differences observed between males and females in their wing and flight muscle allometries cannot be attributed solely to the presence or absence of horns. Nevertheless, without a priori knowledge of the optimal scaling relationships for wing and flight muscle size, we argue that the naturally hornless females represent an appropriate (albeit not perfect) baseline for assessing whether males compensate for their handicap of bearing exaggerated horns.

A second limitation is that the beetles used in this study may have experienced relatively benign conditions: The beetles used in our flight measurements were collected from a university campus and the beetles used in our morphometric analyses were purchased as final instar larvae from a commercial supplier and raised to adulthood in the lab. However, we doubt that the conditions experienced by our beetles were sufficient to mask any costs of carrying or producing horns. In particular, we found no differences in the relationships between horn length and body size among our lab-reared beetles, the beetles collected on the campus grounds, and beetles from a rural population that was monitored briefly as a side project. We therefore suspect that the wing and flight muscle allometries that we measured in the lab-reared beetles are representative of the allometries found in natural beetle populations. Additionally, we have no evidence that the beetles living on campus grounds fly differently than beetles that developed in more natural conditions. The flight speeds reported here on our urban

population of *T. dichotomus* are similar to the flight speeds measured on a wild beetle population (Hongo 2010). Although the wild-caught beetles flew slightly slower than our urban beetles, the previous study measured flight speed on tethered males, while we measured flight speed on unencumbered, free-flying beetles. As a result, the differences in flight performance between the 2 studies are probably primarily due to different methodologies rather than inherent differences in the beetles' condition. More importantly, the basic conclusion of both studies is the same: Long horns do not make it more difficult to fly.

A central tenet of sexual selection theory is that ornaments and weapons are costly (reviewed in Andersson 1994). Rhinoceros beetle horns are among the largest sexually selected traits found in Nature (Darwin 1871; Eberhard 1980; Andersson 1994), and we expect these extreme morphologies to be associated with particularly high fitness costs. Contrary to our expectations that the long pitchfork-like horn of male *T. dichotomus* makes flying more cumbersome, here, we have shown that the horns do not impose significant flight costs. Given the importance of costs for both maintaining the reliability of ornaments and weapons as signals of male quality, and ultimately for limiting maximum trait size, future work will be needed to investigate other potential costs (e.g., weakened immunity, increased predation, resource allocation tradeoffs) that may have been important in shaping the evolution of these extreme horn morphologies.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>.

FUNDING

Ford Foundation; National Science Foundation (OISE 0912433 and DGE 0809127 to E.L.M.).

We thank D. Tuss for the beetle illustrations and B. Tobalske and K. Dial for letting us use the radar gun. We are grateful to L. W. Chang, Y. T. Chen, C. P. Lin, S. F. Lo, and P. F. Pai for their assistance in Taiwan. C. Allen, R. Knell, J. Smith, B. Tobalske, A. Woods, and an anonymous reviewer provided valuable comments on earlier versions of the manuscript.

REFERENCES

- Allen BJ, Levinton JS. 2007. Costs of bearing a sexually selected ornamental weapon in a fiddler crab. *Funct Ecol*. 21:154–161.
- Andersson M. 1994. *Sexual selection*. Princeton (NJ): Princeton University Press.
- Andersson S, Andersson M. 1994. Tail ornamentation, size dimorphism and wing length in the genus *Euplectes* (Ploceinae). *Auk*. 111:80–86.
- Balmford A, Jones IL, Thomas ALR. 1994. How to compensate for costly sexually selected tails: the origin of sexually dimorphic wings in long-tailed birds. *Evolution*. 48:1062–1070.
- Barbosa A, Møller AP. 1999. Aerodynamic costs of long tails in male barn swallows *Hirundo rustica* and the evolution of sexual size dimorphism. *Behav Ecol*. 10:128–135.
- Basolo AL, Alcaraz G. 2003. The turn of the sword: length increases male swimming costs in swordtails. *Proc R Soc Lond B Biol Sci*. 270:1631–1636.
- Buchanan KL, Evans MR. 2000. The effect of tail streamer length on aerodynamic performance in the barn swallow. *Behav Ecol*. 11:228–238.
- Clark CJ, Dudley R. 2009. Flight costs of long, sexually selected tails in hummingbirds. *Proc R Soc B Biol Sci*. 276:2109–2115.
- Crawley MJ. 2007. *The R book*. Chichester (UK): John Wiley and Sons.

- Darwin C. 1871. The descent of man, and selection in relation to sex. London: John Murray.
- Eberhard WG. 1980. Horned beetles. *Sci Am.* 242:166–182.
- Eberhard WG, Gutierrez EE. 1991. Male dimorphisms in beetles and earwigs and the question of developmental constraints. *Evolution.* 45:18–28.
- Emlen DJ. 1997. Alternative reproductive tactics and male-dimorphism in the horned beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Behav Ecol Sociobiol.* 41:335–341.
- Emlen DJ. 2001. Costs and the diversification of exaggerated animal structures. *Science.* 291:1534–1536.
- Evans MR, Thomas ALR. 1992. The aerodynamic and mechanical effects of elongated tails in the scarlet-tufted malachite sunbird: measuring the cost of a handicap. *Anim Behav.* 43:337–347.
- Folstad I, Karter AJ. 1992. Parasites, bright males, and the immunocompetence handicap. *Am Nat.* 139:603–622.
- Godin J-GJ, McDonough HE. 2003. Predator preference for brightly colored males in the guppy: a viability cost for a sexually selected trait. *Behav Ecol.* 14:194–200.
- Grafen A. 1990. Biological signals as handicaps. *J Theor Biol.* 144:517–546.
- Hongo Y. 2003. Appraising behaviour during male-male interaction in the Japanese horned beetle *Trypoxylus dichotomus septentrionalis* (Kono). *Behaviour.* 140:501–517.
- Hongo Y. 2007. Evolution of male dimorphic allometry in a population of the Japanese horned beetle *Trypoxylus dichotomus septentrionalis*. *Behav Ecol Sociobiol.* 62:245–253.
- Hongo Y. 2010. Does flight ability differ among male morphs of the Japanese horned beetle *Trypoxylus dichotomus septentrionalis* (Coleoptera: Scarabaeidae)? *Ethol Ecol Evol.* 23:271–279.
- Hongo Y, Kaneda H. 2009. Field observations of predation by the Ural Owl *Strix uralensis* upon the Japanese horned beetle *Trypoxylus dichotomus septentrionalis*. *J Yamashina Inst Ornithol.* 40:90–95.
- Husak JF, Swallow JG. 2011. Compensatory traits and the evolution of male ornaments. *Behaviour.* 148:1–29.
- Iguchi Y. 1998. Horn dimorphism of *Allomyrina dichotoma septentrionalis* (Coleoptera: Scarabaeidae) affected by larval nutrition. *Ann Entomol Soc Am.* 91:845–847.
- Iwasa Y, Pomiankowski A, Nee S. 1991. The evolution of costly mate preferences II. The “handicap” principle. *Evolution.* 45:1431–1442.
- Karino K, Niiyama H, Chiba M. 2005. Horn length is the determining factor in the outcomes of escalated fights among male Japanese horned beetles, *Allomyrina dichotoma* L. (Coleoptera: Scarabaeidae). *J Insect Behav.* 18:805–815.
- Kawano K. 1995. Horn and wing allometry and male dimorphism in giant rhinoceros beetles (Coleoptera: Scarabaeidae) of tropical Asia and America. *Ann Entomol Soc Am.* 88:92–99.
- Kawano K. 1997. Cost of evolving exaggerated mandibles in stag beetles (Coleoptera: Lucanidae). *Ann Entomol Soc Am.* 90:453–461.
- Kawano K. 2006. Sexual dimorphism and the making of oversized male characters in beetles (Coleoptera). *Ann Entomol Soc Am.* 99:327–341.
- Kirkpatrick M. 1982. Sexual selection and the evolution of female choice. *Evolution.* 36:1–12.
- Knell RJ. 2009. On the analysis of non-linear allometries. *Ecol Entomol.* 34:1–11.
- Kodric-Brown A, Brown JH. 1984. Truth in advertising: the kinds of traits favored by sexual selection. *Am Nat.* 124:309–323.
- Kotiaho JS. 2001. Costs of sexual traits: a mismatch between theoretical considerations and empirical evidence. *Biol Rev.* 76:365–376.
- Lande R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution.* 34:292–305.
- Madewell R, Moczek AP. 2006. Horn possession reduces maneuverability in the horn-polyphenic beetle, *Onthophagus nigriventris*. *J Insect Sci.* 6:21.
- Marden JH. 1987. Maximum lift production during takeoff in flying animals. *J Exp Biol.* 130:235–258.
- Moczek AP, Emlen DJ. 2000. Male horn dimorphism in the scarab beetle, *Onthophagus taurus*: do alternative reproductive tactics favour alternative phenotypes? *Anim Behav.* 59:459–466.
- Møller AP. 1996. The cost of secondary sexual characters and the evolution of cost-reducing traits. *Ibis.* 138:112–119.
- Møller AP, De Lope F, Saino N. 1995. Sexual selection in the barn swallow *Hirundo rustica*. VI. Aerodynamic adaptations. *J Evol Biol.* 8:671–687.
- Møller AP, Hedenström A. 1999. Comparative evidence for costs of secondary sexual characters: adaptive vane emargination of ornamented feathers in birds. *J Evol Biol.* 12:296–305.
- Møller AP, Nielsen JT. 1997. Differential predation cost of a secondary sexual character: sparrowhawk predation on barn swallows. *Anim Behav.* 54:1545–1551.
- Muggeo VMR. 2003. Estimating regression models with unknown break-points. *Stat Med.* 22:3055–3071.
- Norberg RA. 1994. Swallow tail streamer is a mechanical device for self deflection of tail leading edge, enhancing aerodynamic efficiency and flight manoeuvrability. *Proc R Soc B Biol Sci.* 257:227–233.
- Nur N, Hasson O. 1984. Phenotypic plasticity and the handicap principle. *J Theor Biol.* 110:275–297.
- Oufiero CE, Garland T. 2007. Evaluating performance costs of sexually selected traits. *Funct Ecol.* 21:676–689.
- Plaistow SJ, Tsuchida K, Tsubaki Y, Setsuda K. 2005. The effect of a seasonal time constraint on development time, body size, condition, and morph determination in the horned beetle *Allomyrina dichotoma* L. (Coleoptera: Scarabaeidae). *Ecol Entomol.* 30:692–699.
- Rantala MJ, Vainikka A, Kortet R. 2003. The role of juvenile hormone in immune function and pheromone production trade-offs: a test of the immunocompetence handicap principle. *Proc R Soc Lond B Biol Sci.* 270:2257–2261.
- Ribak G, Pitts ML, Wilkinson GS, Swallow JG. 2009. Wing shape, wing size, and sexual dimorphism in eye-span in stalk-eyed flies (Diptera: Diopsidae). *Biol J Linn Soc.* 98:860–871.
- Ribak G, Swallow J. 2007. Free flight maneuvers of stalk-eyed flies: do eye-stalks affect aerial turning behavior? *J Comp Physiol A Neuroethol Sens Neural Behav Physiol.* 193:1065–1079.
- Saino N, Møller AP. 1996. Sexual ornamentation and immunocompetence in the barn swallow. *Behav Ecol.* 7:227–232.
- Searcy WA, Nowicki S. 2005. The evolution of animal communication: reliability and deceptibility in signaling systems. Princeton (NJ): Princeton University Press.
- Siva-Jothy M. 1987. Mate securing tactics and the cost of fighting in the Japanese horned beetle, *Allomyrina dichotoma* L. (Scarabaeidae). *J Ethol.* 5:165–172.
- Stearns S. 1992. The evolution of life histories. Oxford: Oxford University Press.
- Swallow JG, Wilkinson GS, Marden JH. 2000. Aerial performance of stalk-eyed flies that differ in eye span. *J Comp Physiol B Biochem Syst Environ Physiol.* 170:481–487.
- Thomas ALR. 1993. On the aerodynamics of birds’ tails. *Philos Trans R Soc Lond B Biol Sci.* 340:361–380.
- Tomkins JL, Kotiaho JS, LeBas NR. 2005. Phenotypic plasticity in the developmental integration of morphological trade-offs and secondary sexual trait compensation. *Proc R Soc B Biol Sci.* 272:543–551.
- Verhulst S, Dieleman SJ, Parmentier HK. 1999. A tradeoff between immunocompetence and sexual ornamentation in domestic fowl. *Proc Natl Acad Sci U S A.* 96:4478–4481.
- Warton DI, Wright IJ, Falster DS, Westoby M. 2006. Bivariate line-fitting methods for allometry. *Biol Rev.* 81:259–291.
- Worthington AM, Swallow JG. 2010. Gender differences in survival and antipredatory behavior in stalk-eyed flies. *Behav Ecol.* 21:759–766.
- Zahavi A. 1975. Mate selection: selection for a handicap. *J Theor Biol.* 53:205–214.
- Zeh DW, Zeh JA. 1988. Condition-dependent sex ornaments and field tests of sexual-selection theory. *Am Nat.* 132:454–459.
- Zuk M, Kolluru GR. 1998. Exploitation of sexual signals by predators and parasitoids. *Q Rev Biol.* 73:415–438.