

Performance is no proxy for genetic quality: trade-offs between locomotion, attractiveness, and life history in crickets

SIMON P. LAILVAUX,^{1,2,3} MATTHEW D. HALL,¹ AND ROBERT C. BROOKS¹

¹Evolution and Ecology Research Centre and School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, New South Wales 2052 Australia

²Department of Biological Sciences, University of New Orleans, 2000 Lakeshore Drive, New Orleans, Louisiana 70148 USA

Abstract. The genetic relationships among traits contributing to overall fitness are an important subject of inquiry because such relationships influence how suites of traits respond to selection. Within the field of sexual selection, these relationships are also of interest for assessing whether any given trait can be used as a proxy for total fitness. A growing number of studies have demonstrated close links between whole-organism performance traits and determinants of individual fitness; however, an understanding of the genetic relationships between performance and important aspects of genetic quality is currently lacking. We present the results of a quantitative genetic study in which we estimate covariation between a locomotor performance trait (maximal jumping ability), calling effort, sexual attractiveness, and life-history traits in male *Teleogryllus commodus* crickets. We show that the major axis of genetic variation (\mathbf{g}_{\max}) is characterized by a contrast between jump performance and life-history traits associated with mating success. Moreover, two additional axes of significant multivariate genetic variation exist, each characterized by strong contrasts among traits. These results argue against the existence of a single axis representing genetic quality, favoring instead the idea that resource allocation strategies shape multiple dimensions of genetic quality through trade-offs among key life-history traits, including performance.

Key words: field cricket; genetic quality; life-history; New South Wales, Australia; performance; sexual selection; *Teleogryllus commodus*; whole-organism performance.

INTRODUCTION

The sexual selection literature reveals a keen interest in the idea of genetic quality (segregating genetic variation in total fitness) and the idea that males signal this quality to females via their displays and ornaments. Female mating preferences for displaying or highly ornamented males are thought to evolve because their offspring inherit both the preference and their sire's genetic quality; subsequent selection on offspring quality then favors the preference via indirect selection (Fisher 1930, Zahavi 1975, Andersson 1994, Kokko et al. 2003). Total fitness, however, is inherently difficult, if not impossible, to measure, particularly when indirect selection explicitly concerns transgenerational fitness (Hunt et al. 2004b). Consequently, researchers have long sought proxies for total fitness that do not require intensive sampling or detailed knowledge of individual paternity. Longevity is often interpreted as such a proxy, but it is problematic, not least because it often trades off against reproduction in early adulthood (Hansen and Price 1995, Brooks and Kemp 2001). For example, male

Teleogryllus commodus crickets that spend more time calling to attract females have significantly shorter life spans when maintained in the laboratory, but are likely to attain greater lifetime reproductive success than males that live longer but invest less in sexual advertisement (Hunt et al. 2004a). Given the trade-offs between reproduction and survival, instantaneous or short-term sexual signaling might be considered to be a more reliable indicator of fitness than longevity; however, "snapshots" of individual quality are again potentially confounded by life-history trade-offs, particularly if investment in advertisement changes over an individual's lifetime (Kokko 1997).

Several authors have recently pointed out that the most important fitness relationships may involve aspects of physiological ecology, including how well an organism performs physiologically (Badyaev 2004, Lailvaux and Irschick 2006a, Irschick et al. 2007b). Whole-organism performance (defined specifically as any quantitative measure of an organism conducting a dynamic, ecologically relevant task; see Irschick and Garland 2001, Lailvaux and Irschick 2006a), in particular, has been the subject of extensive investigation, partly due to the ease of measurement of many common performance traits (reviews in Bennett and Huey 1990, Irschick and Garland 2001, Irschick et al. 2008). In addition to the demonstrated importance of performance traits, such as locomotor capacities, to fitness and

Manuscript received 1 June 2009; revised 28 August 2009; accepted 31 August 2009. Corresponding Editor: S. J. Simpson.

³ Present address: Department of Biological Sciences, University of New Orleans, 2000 Lakeshore Drive, New Orleans, Louisiana 70148 USA.
E-mail: slailvaux@gmail.com

survival (Irschick et al. 2007a, 2008, Calsbeek and Smith 2008), recent years have seen increasing integration between performance and sexual selection, with a growing number of studies illustrating the functional relevance of performance traits to sexual selection (and particularly male competition) in animal taxa ranging from lizards to crabs and beetles (reviews in Lailvaux and Irschick 2006a, Husak and Fox 2008). These studies and others have shown that performance traits often have a considerable impact on individual reproductive success. For example, several studies have shown that performance traits such as jumping ability and bite force predict male combat outcomes in species with female-defense polygyny-type mating systems (Lailvaux et al. 2004, Huyghe et al. 2005, Lappin and Husak 2005, Lailvaux and Irschick 2007), and male sprinting performance predicts realized offspring number in the lizard *Crotaphytus collaris* (Husak et al. 2006), again probably because fast sprinters are better able to defend females against rival males in this species (Husak et al. 2008; see also Husak et al. [2009], who showed that bite force also predicts offspring number in collared lizards).

Although the role of performance in male combat has been moderately studied, we currently lack a clear understanding of the role of male performance in the context of female mate choice. The few studies that have attempted to address this issue have found either mixed evidence that females prefer good performers (Lailvaux and Irschick 2006b, Snowberg and Benkman 2009), or indirect links between female preferences and male performance via sexually selected signals or displays (Nicoletto 1991, 1993, Takahashi and Kohda 2004). The question of whether females mate preferentially with high-performance males is pertinent because such a preference would suggest an important pathway via which indirect selection might act on mating preferences. If such a pattern were general and if whole-organism performance is indeed a useful general correlate of overall fitness, then performance measures may act as a convenient index of male genetic quality. This would constitute a methodological breakthrough for ecological and sexual selection studies because whole-organism performance traits such as locomotion are easily measured in a wide range of taxa.

However, despite the potential importance of performance as a predictor of organismal fitness (and thus genetic quality) in nature, two important limitations remain. First, until recently, few studies had attempted to integrate performance into a life-history framework (reviews in Bennett and Huey 1990, Ghalambor et al. 2003, Guerra and Pollack 2009; for examples see Veasey et al. 2001, Royle et al. 2006). Second, fewer still have explored the underlying quantitative genetics. The combination of life-history theory and quantitative genetics provides the necessary framework within which to understand the evolutionary significance of performance measures, in general, and how genetic quality relates to the physiological performance capabilities of

an organism, in particular. Rather than viewing male quality as the expression of a single trait, the fitness consequences of a trait are now viewed in terms of trade-offs with other fitness traits and the underlying genetic architecture that mediates these trade-offs (Kokko 1998, Blows and Hoffmann 2005, Kokko et al. 2006, Blows 2007). Although most of this work has considered the trade-offs between reproductive effort (including display and ornament expression) and longevity (e.g., Brooks 2000, Hunt et al. 2006), the potential relationships between these traits and physiological performance have received little attention (Badyaev 2004, Lailvaux and Irschick 2006a, Irschick et al. 2007b). Both studies of performance and studies of male genetic quality therefore stand to benefit substantially from the integration of whole-organism performance within a life-history and quantitative genetic framework.

In this study, we seek to integrate whole-organism performance with an understanding of genetic quality in the context of both sexual signaling and life span. Given the difficulties inherent in obtaining a measure of total fitness, we measured several key fitness components that are known determinants of overall genetic quality. We adopted a multivariate quantitative genetic approach to test the prediction that a whole-organism performance trait (maximal jumping ability) would be strongly and positively correlated with a range of fitness components, including life-history traits (development rate and adult longevity) and reproductive investment (calling effort and attractiveness to females in close-quarters courtship), in at least one significant dimension of multivariate genetic variation in the black field cricket *Teleogryllus commodus*. In doing so, we assess the idea that physiological performance may be a useful general proxy for empiricists wishing to estimate fitness and genetic quality. Although we note that several types of whole-organism performance could be considered, based on the general definition we have just provided, we concentrate in this paper on locomotor performance, given the known links between locomotor traits and overall fitness in other animal taxa. Furthermore, maximum locomotor performance capacities such as jumping ability require maximal effort, and sum the output of several complex functional systems (Lailvaux and Irschick 2006a). Jump performance has also been shown to be important for escape from predators in crickets (Dangles et al. 2007) and plays an important role in determining the outcomes of male-male combat interactions in *T. commodus* (Hall et al., *in press*). Measuring jumping performance therefore captures an additional potential element of overall “male quality” in this species. Finally, both the phenotypic and genetic relationships among elements of male attractiveness and life-history traits have been well-studied in these crickets (Hunt et al. 2004a, 2006, Zajitschek et al. 2007, Hall et al. 2008). Thus, *T. commodus* is an ideal organism for addressing questions relating to life history, sexual attractiveness, and locomotor performance from the perspective of quantitative genetics.

METHODS

The laboratory stock used for this experiment were the fourth-generation offspring of a culture originating from Smiths Lake (32°22' S, 152°30' E), New South Wales, Australia. As part of a parental half-sib breeding design, we mated 54 sires to six dams each, although nine males died before completing the planned six matings and 43 dams failed to produce offspring. From the resulting 237 full-sib families, we collected 25 offspring and reared them individually from hatching in plastic containers (7 × 7 × 5 cm) provided with food (Friskies Go-Cat Senior, Nestlé Australia, Sydney, Australia) and water *ad libitum*, with a piece of egg carton for shelter. We replaced food and water each week and kept the crickets in a constant-temperature room (28°C, 14:10 h light:dark regime) where the positions of the containers within the room were randomized weekly to minimize local environmental effects. Each day we checked the individuals for eclosions and monitored survival.

Measuring reproductive investment

To characterize male reproductive investment, we estimated for each male its pre-copulatory attractiveness and nightly investment in calling. Male attractiveness was estimated by mating males with a randomly chosen female from within the same breeding design and observing their courtship behavior (following Shackleton et al. 2005a). We conducted the trials every three days, using crickets that were between 10 and 12 days post-eclosion. For each trial we placed a mating pair in an arena consisting of a plastic container (17 × 12 × 8 cm) lined with damp paper towels. The trials began in the first two hours after dark in a room dimly lit by red incandescent light (40 W, Philips Lighting, Eindhoven Pays-Bas, The Netherlands), in order to minimize observer disturbance. From the mating trials, we estimated a male's attractiveness as the inverse of the time taken from the start of the trial until the female mounted the male. Using a custom-built electronic monitoring device, we also measured for each male the time spent calling during an evening. This device monitors up to 192 acoustically isolated males 10 times per second, with a male considered to have called during any given second if one or more of the 10 samples registered a call. We monitored male calling over a 12-h period per night approximately every 4 days, beginning at 5 days post-eclosion. For a given male, we used his average time spent calling each night in seconds as our estimate of calling effort. In total, we were able to estimate the pre-copulatory attractiveness and average calling effort for 924 males.

Measuring physiological performance

We measured jumping performance in male *T. commodus* using standard methods. Following Hall et al. (*in press*), we used a Fastec high-speed camera with a frame rate of 500 frames per second (Fastec Imaging,

San Diego, California, USA) to capture video clips of crickets jumping unassisted off of a designated jump platform. A mirror placed at a 45° angle above the jump platform allowed us to film both dorsal and lateral views simultaneously. We later merged the two two-dimensional jump trajectories into a single three-dimensional view of each jump using Pythagoras's rule. We used a 1 × 1 cm grid taped behind the jump platform for scale. Each individual was jumped at least five times, and the best jumps were retained for analysis (for justification of the use of maximum values in performance studies, see Losos et al. 2002, Adolph and Pickering 2008). To quantify jump performance from video footage, we digitized the position of the crickets in each frame using ProAnalyst v. 1.5.1.9 (Xcitex, Cambridge, Massachusetts, USA). Given that there was little or no rotation of the head in most jumps, we digitized only the center of the head during each jump (Marsh and John-Alder 1994). Note also that our large sample size for the jump measures (817 individuals) and the time burden required to digitize multiple movies per individual precluded the digitization of several points for each jump.

We began digitizing 20 frames before the first movement, and stopped when the cricket either hit a wall or left the frame. We used a zero phase-shift Butterworth filter (Winter 2005) to smooth the *x*, *y*, and *z* co-ordinates thus obtained, and calculated instantaneous velocity and acceleration from the smoothed displacements. Mass-specific power was obtained by multiplying the instantaneous velocity and acceleration profiles (following Toro et al. 2003, 2004, Bergmann and Irschick 2006, Vanhooydonck et al. 2006; Hall et al., *in press*). As an additional variable, and as a check on the performance data calculated from high-speed camera footage, we also measured jump distance directly for each jump using a tape measure to the nearest 0.001 m. Because the three jump variables obtained from the video footage were all highly correlated, we used only maximum mass-specific power output and measured jump distance in all analyses to avoid problems with collinearity (Kachigan 1991).

Statistical analysis

The univariate and multivariate genetic analyses were implemented in the MIXED procedure of SAS (Version 9.1: SAS Institute, Cary, North Carolina, USA) using REML (restricted maximum likelihood estimation) to estimate the variance components as part of a standard half-sib nested model. Before analysis, attractiveness was transformed using natural logarithms, while calling effort and jump power were cube-root and square-root transformed, respectively. We first used a univariate model to estimate the narrow sense heritabilities for each trait. Significance of heritabilities was determined by re-running the model with the sire variance component removed, and then comparing the difference in the log likelihood values with a chi-square test and one degree of freedom. In the case of the heritabilities, we halved

TABLE 1. Univariate statistics describing phenotypic and genetic variability for the measures of physiological performance, life span, development, and reproductive investment for male field crickets, *Teleogryllus commodus*.

Measurement	Mean	SD	h^2	CV_A
Jump distance (m)	0.452	0.134	0.322***	16.837
Jump power ($^2\sqrt{[W/kg]}$)	1.787	0.638	0.302**	19.559
Life span (days)	44.830	14.154	0.411***	20.959
Development rate (days $\times 10^{-2}$)	1.968	0.165	0.252*	4.255
Attractiveness ($\log_e[s^{-1}]$)	-6.248	1.293	0.227**	9.880
Calling effort ($^3\sqrt{[s]}$)	14.423	5.478	0.305***	20.960

Notes: The univariate statistics reported include the phenotypic mean and standard deviations, the narrow-sense heritabilities (h^2), and the additive genetic coefficients of variation (CV_A). Attractiveness was estimated by mating males with randomly chosen females from the breeding design and observing courtship behavior; calling effort was estimated by measuring how often adult males called each night every four days.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

the resulting probabilities to obtain the significance level as the variance components are constrained to be greater than zero (Saxton 2004). To complement our heritability estimates, we also compared evolvability between traits by calculating the additive genetic coefficient of variation for each trait ($CV_A = 100([\sqrt{V_A}]/\bar{X})$, (Houle 1992).

Finally, a multivariate model was used to estimate the six-dimensional genetic variance-covariance (**G**) matrix. Before analysis, we standardized all traits to a mean of 0 and a standard deviation of 1. We determined the statistical support for each of the genetic dimensions using factor-analytic modeling (Hine and Blows 2006), whereby we sequentially dropped dimensions from a factor analytic model at the sire level as implemented in the MIXED procedure. We then used a series of nested log-likelihood ratio tests to determine when the dropping of a dimension resulted in a significantly worse fit and, therefore, the statistical support for the presence of the dropped dimension. Inclusion of body size in the analyses returned very similar results to those without body size, but did not add any heuristic value. We therefore excluded body size from the final analyses.

RESULTS

To characterize the genetic basis of jumping performance in *T. commodus*, we first estimated both the heritabilities and the additive genetic coefficients of variation (Table 1). Both jump distance and jump power displayed significant heritabilities, indicating that ~30% of the phenotypic variance in jumping ability can be explained by additive genetic effects. The heritabilities for our two measures of jumping ability were also

roughly equal to the other measured traits, as all traits showed significant heritability ranging from 22% for attractiveness to 41% for life span. Moreover, the additive genetic coefficients of variation indicate that the potential evolvability of jumping ability is much higher than development rate and attractiveness and almost equivalent to calling effort and life span. Examination of the genetic variance-covariance (**G**) matrix (Table 2) revealed two important genetic relationships between our estimates of jumping ability (jump distance and jump power), life history (development rate and life span), and reproductive investment (attractiveness and calling effort). First, the relatively high genetic covariance between the two independent measures of jump performance suggests that our estimates of jumping ability agree with each other closely, and these measurements are therefore robust. Second, the patterns of genetic covariance appear to describe two separately segregating groups of variables, because jump distance, jump power, and life span all covary positively with each other, but covary negatively with development rate, attractiveness, or calling effort.

The patterns of genetic covariance between traits are formally characterized by the eigenanalysis of **G** (Table 3), where factor-analytic modeling indicated strong statistical support for the presence of three genetic dimensions accounting for 86.7% of the estimated genetic variance (log-likelihood ratio test: $\chi^2 = 10.8$, $df = 4$, $P = 0.029$). The major eigenvector of **G**, known as g_{max} , accounted for 45.4% of the estimated genetic variance, and represents the negative genetic association between two groups of traits: jump distance, jump

TABLE 2. Additive genetic variance-covariance (**G**) matrix for measures of physiological performance, life span, development, and reproductive investment for male *T. commodus*.

Measurement	Jump distance	Jump power	Life span	Development rate	Attractiveness	Calling effort
Jump distance	0.314					
Jump power	0.303	0.293				
Life span	0.108	0.101	0.101			
Development rate	-0.120	-0.047	-0.164	0.266		
Attractiveness	-0.062	-0.042	-0.144	0.078	0.203	
Calling effort	-0.014	-0.038	-0.069	0.185	-0.009	0.315

Note: The genetic variances of standardized traits are presented along the diagonal in boldface, and the genetic covariances are below the diagonal.

TABLE 3. Eigenvectors and eigenvalues (λ_n) of \mathbf{G} for standardized measures of physiological performance, life span, development, and reproductive investment in *T. commodus*.

Measurement	\mathbf{g}_{\max}	\mathbf{g}_2	\mathbf{g}_3	\mathbf{g}_4	\mathbf{g}_5	\mathbf{g}_6
Jump distance	-0.506	0.466	-0.181	-0.093	-0.258	-0.647
Jump power	-0.456	0.486	-0.222	0.137	0.316	0.623
Life span	-0.502	-0.275	0.619	0.529	0.061	-0.079
Development rate	0.410	0.409	0.139	0.311	0.644	-0.366
Attractiveness	0.221	0.040	-0.415	0.769	-0.430	0.032
Calling effort	0.260	0.549	0.587	-0.064	-0.480	0.229
λ_n	0.826	0.440	0.310	0.157	0.085	-0.024
Variation (%)	45.4	24.2	17.1	8.6	4.7	0

Notes: Each \mathbf{g} represents a dimension of genetic variation; \mathbf{g}_{\max} is the same as \mathbf{g}_1 , but the convention is to refer to it as \mathbf{g}_{\max} ; λ_n represents the eigenvalue for a given variable, n .

power, and life span, which all loaded negatively on \mathbf{g}_{\max} , vs. development time, calling effort, and attractiveness, which all loaded positively. However, the relatively high dimensionality of this data set argues against the existence of a single or few dimensions of genetic quality. Furthermore, the contrasting loadings on the remaining two other dimensions (\mathbf{g}_2 and \mathbf{g}_3) suggest that the relationship between jumping performance and the other measured life-history traits is probably complex, albeit dominated by the trade-offs between jumping performance and the major determinants of reproductive success as observed in \mathbf{g}_{\max} .

DISCUSSION

Whole-organism performance studies in ecology often suggest (Lailvaux and Irschick 2006a) or empirically demonstrate (e.g., Husak et al. 2006, 2009) that such performance is closely tied to fitness in terms of overall number of offspring. This has led to the suggestion that measures of performance may represent a valuable proxy for genetic quality (Lailvaux and Irschick 2006b), particularly because dynamic performance measures such as locomotor ability are predicted to closely capture the output from a complex functional system encompassing physiological states such as fat stores, metabolic rates, and circulating nutrient levels (Garland 1984, Bennett and Huey 1990). This idea, however, has remained largely untested due to the lack of studies describing both the quantitative genetic basis of performance and the genetic relationships between performance and other key life-history traits.

In this study, we examined the quantitative genetics of whole-organism locomotor performance, male reproductive investment, development, and life span in the black field cricket, *Teleogryllus commodus*. We found that substantial additive genetic variation exists for the multiple estimates of male jumping performance, and that the evolvability of these traits is approximately equal to those of life span and male nightly calling, which appears to be the most important determinant of male fitness (Table 1). Furthermore, the strong positive genetic covariance between jump distance and jump power (Table 2) indicates that genetically, at least, these two measures of jumping performance are likely to be

largely the same trait. Together these results indicate that selection operating directly on male jumping performance has a strong potential to result in evolutionary change. However, the positive genetic covariance between jumping performance and life span and the negative covariances between these two traits and development rate, attractiveness, and calling effort (Table 2) indicate that no single trait, including jumping performance, will capture genetic quality alone. Instead, our results indicate that the relationships between whole-organism performance, genetic quality, and other life-history traits are complex and subject to genetic trade-offs in much the same way as life-history traits are. This finding has important implications for: (1) the potential of whole-organism performance to impact on the question of mate choice evolution by indirect selection and (2) the dimensionality of genetic quality in combinations of life-history traits.

Performance, life history, and indirect benefits

The question of whether traits that influence male mating success also signal whole-organism performance is important because such a relationship would provide the genetic basis for the evolution of mate choice via indirect selection, one of the more persistent areas of controversy in evolutionary biology (Kirkpatrick and Ryan 1991, Kirkpatrick 1996, Kirkpatrick and Barton 1997, Kokko et al. 2003). If whole-organism performance is genetically correlated with male attractiveness (as suggested by Nicoletto 1991, 1993, Alatalo et al. 1998), and if the offspring of females that mate with attractive males therefore enjoy improved fitness (including physiological performance) due to paternally inherited genes, this would present a mechanism for indirect selection on mate choice that is at once powerful, ecologically relevant, and easy for the empiricist to measure. However, while indirect evidence for the genetic link between performance and male attractiveness has come from studies showing a correlation between offspring performance and the sexual traits of a sire (e.g., Evans et al. 2004), few studies have characterized both the quantitative genetic basis of performance and the pattern of genetic covariation

between whole-organism performance and traits underpinning male attractiveness to females.

In our study on *T. commodus*, we found no evidence that estimates of attractiveness or calling effort were positively genetically associated with jumping performance. Instead we found evidence for strong negative genetic relationships between male mating success and jumping ability. The major axis of genetic variation (g_{\max}), which accounts for ~45% of the estimated genetic variation in all traits, represents a clear contrast between calling effort, development time, and attractiveness on the one hand, and jumping performance and life span on the other (Table 3). Given the previously established importance of calling effort and attractiveness as key determinants of acquiring mates for male *T. commodus* in both the laboratory and field (Hunt et al. 2004a, Shackleton et al. 2005b, Bentsen et al. 2006, Zajitschek et al. 2007), these results suggest that the largest proportion of genetic variance comprises a strong trade-off between longevity and performance on one hand, and reproductive success and fast development on the other. It is possible that the contrast between jumping performance and calling effort may reflect a genetic trade-off between burst performance (jumping and its correlates) and endurance (calling and its correlates), a possibility that remains to be formally tested. These data are consistent with dramatic phenotypic (Hunt et al. 2004a) and genetic (Hunt et al. 2006) trade-offs between longevity and calling effort observed in previous studies, and provide the first direct evidence of a genetic trade-off between reproductive success and a locomotor performance trait.

Together our findings indicate that it is unlikely that females will gain indirect genetic benefits in the terms of offspring performance by mating with attractive males in *T. commodus*. Males that, for example, mate quickly and invest heavily in nightly calling will not necessarily produce sons with superior jumping capabilities. Our finding here that jumping performance exhibits both positive and negative relationships with life-history variables such as development rate and calling effort is also consistent with those of previous studies that have examined whole-organism performance from a life-history perspective (Ghalambor et al. 2003). It therefore appears likely that similar whole-organism performance traits in other species will be subject to the same multivariate life-history trade-offs as occur among life span, reproductive investment, and development rate.

Although whole-organism performance has become increasingly integrated with life-history approaches in phenotypic terms, the genetic relationships among locomotor performance and various life-history traits have received little attention (Roff and Fairbairn 2007). Using simple bivariate approaches, previous authors have reported either no (Gu and Barker 1995) or positive genetic correlations (Dingle 1991) between tethered flight duration and life-history traits such as development time and fecundity in two species of

Drosophila (*D. aldrichi* and *D. buzzatii*) and in the milkweed bug *Oncopeltus fasciatus*, respectively. However, no genetic studies to our knowledge have used multivariate analyses to examine the relationships among performance and key life-history traits relating to reproduction, and hence placing our results here within an appropriate comparative context is currently problematic. Given that the utility of bivariate analyses to uncover interpretable patterns of correlations within multitrait systems is inherently limited (Blows and Hoffmann 2005), we advocate the use of appropriate multivariate techniques in future studies of both genetic quality and of life-history trade-offs involving whole-organism performance.

The dimensionality of genetic quality

The idea of indirect genetic benefits to female choice is consistent with the concept of one or more major dimensions of overall genetic quality, along which most, if not all, major fitness components are aligned. Female choice for males at the positive end of such a dimension would deliver unambiguous genetic benefits. However, the quantitative genetics of life histories and the nature of trade-offs hinge on the relative amounts of genetic variation in acquisition and allocation of resources (Houle 1991). Where a high proportion of genetic variance is due to differences in resource acquisition, one expects large positive genetic correlations among traits, whereas negative correlations indicate allocational trade-offs under similar total resource levels. This idea underpins the idea that sexual signals may capture genome-wide genetic variation in allocation via the mechanism of condition-dependent expression (Andersson 1994, Rowe and Houle 1996). Under condition dependence, individuals in good condition (i.e., that have acquired resources successfully) exceed their poor-condition cohorts in most, if not all, life-history traits, especially key traits relating to development, survival, and attractiveness that might impact on overall fitness. Implicit in the idea that sexual signals indicate total fitness is an assumption that these major axes of genetic variation are dominated by positive genetic correlations between most traits, but particularly between condition-dependent traits affecting reproductive success and performance.

Our results indicate three dimensions of significant genetic variation, all of which are characterized by strong trade-offs between traits. This does not support the prediction that there should be few significant dimensions that characterize general genetic quality. The pattern that we observed is expected when most of the genetic variance expressed is due to differences in resource allocation to different functions, rather than differences in the overall allocation of resources (Houle 1991). This suggests that the multiple dimensions of genetic variation may be shaped by the different allocation strategies that individuals with different genotypes employ to maximize their own fitness. In *T.*

commodus, for example, one potential factor that may be shaping the different patterns of genetic variation is the contrasting patterns of selection imposed by male combat vs. female choice. For example, although jumping capabilities have been shown to play an important role in determining the winner of male combat (Hall et al., *in press*), females do not prefer to mate with males that win fights (Shackleton et al. 2005b). Rather than attempting to characterize genetic quality in terms of a simple linear combination of traits that maximize fitness, our results indicate that there may be multiple dimensions of genetic quality, each shaped by different patterns of allocation.

In summary, our results suggest that jump performance in *T. commodus* is strongly genetically associated with key life-history traits such as longevity, development rate, and male sexual advertisement and male sexual attractiveness, but not in such a way that this performance measure easily describes genetic quality or the indirect genetic benefits to female choice. Instead, we suggest that jump performance will be subject to the same life-history trade-offs as other traits that depend on the allocation and acquisition of resources. Furthermore, the existence of multiple orthogonal dimensions of genetic variation in the *T. commodus* genome, each characterized by strong contrasts between fitness components, suggests that no single dimension of genetic quality exists in this species. We suggest that future studies examining the multivariate genetic relationships among disparate life-history traits will offer important insights into both overall genetic quality and the ecology and evolution of whole-organism performance.

ACKNOWLEDGMENTS

This study was supported by an ARC Discovery grant and APD Fellowship to S. Lailvaux, and by a Discovery Grant and QEII Research Fellowship to R. Brooks. Thanks to Luc Bussière and Duncan Irschick for valuable discussion, Mark Blows for statistical advice, and Elke Venstra for assistance with cricket maintenance. This paper was also greatly improved by comments from two anonymous reviewers.

LITERATURE CITED

- Adolph, S. C., and T. Pickering. 2008. Estimating maximum performance: effects of intraindividual variation. *Journal of Experimental Biology* 211:1336–1343.
- Alatalo, R. V., J. S. Kotiaho, J. Mappes, and S. Parri. 1998. Mate choice for offspring performance: major benefits or minor costs? *Proceedings of the Royal Society of London B* 265:2297–2301.
- Andersson, M. 1994. *Sexual selection*. Princeton University Press, Princeton, New Jersey, USA.
- Badyaev, A. V. 2004. Developmental perspective on the evolution of sexual ornaments. *Evolutionary Ecology Research* 6:975–991.
- Bennett, A. F., and R. B. Huey. 1990. Studying the evolution of physiological performance. Pages 251–284 in D. J. Futuyma and J. Antonovics, editors. *Oxford Surveys in Evolutionary Biology*. Oxford University Press, Oxford, UK.
- Bentsen, C. L., J. Hunt, M. D. Jennions, and R. Brooks. 2006. Complex multivariate sexual selection on male acoustic signaling in a wild population of *Teleogryllus commodus*. *American Naturalist* 167:102–116.
- Bergmann, P. J., and D. J. Irschick. 2006. Effects of temperature on maximum acceleration, deceleration and power output during vertical running in geckos. *Journal of Experimental Biology* 209:1404–1412.
- Blows, M. W. 2007. A tale of two matrices: multivariate approaches in evolutionary biology. *Journal of Evolutionary Biology* 20:1–8.
- Blows, M. W., and A. A. Hoffmann. 2005. A reassessment of genetic limits to evolutionary change. *Ecology* 86:1371–1384.
- Brooks, R. 2000. Negative genetic correlation between male sexual attractiveness and survival. *Nature* 406:67–70.
- Brooks, R., and D. J. Kemp. 2001. Can older males deliver the good genes? *Trends in Ecology and Evolution* 16:308–313.
- Calsbeek, R., and T. B. Smith. 2008. Experimentally replicated disruptive selection on performance traits in a Caribbean lizard. *Evolution* 62:478–484.
- Dangles, O., D. Pierre, J. P. Christides, and J. Casas. 2007. Escape performance decreases during ontogeny in wild crickets. *Journal of Experimental Biology* 219:3165–3170.
- Dingle, H. 1991. Evolutionary genetics of animal migration. *American Zoologist* 31:253–264.
- Evans, J. P., J. L. Kelley, A. Bisazza, E. Finazzo, and A. Pilastro. 2004. Sire attractiveness influences offspring performance in guppies. *Proceedings of the Royal Society B* 271:2053–2042.
- Fisher, R. A. 1930. *The genetical theory of natural selection*. Oxford University Press, Oxford, UK.
- Garland, T. J. 1984. Physiological correlates of locomotory performance in a lizard: an allometric approach. *American Journal of Physiology* 247:R806–R815.
- Ghalambor, C. K., J. A. Walker, and D. N. Reznick. 2003. Multi-trait selection, adaptation, and constraints on the evolution of burst swimming performance. *Integrative and Comparative Biology* 43:431–438.
- Gu, H., and J. S. F. Barker. 1995. Genetic and phenotypic variation for flight ability in the cactophilic *Drosophila* species, *D. aldrichi* and *D. buzzatii*. *Entomologia Experimentalis et Applicata* 76:25–35.
- Guerra, P. A., and G. S. Pollack. 2009. Flight behaviour attenuates the trade-off between flight capability and reproduction in a wing polymorphic cricket. *Biology Letters* 5:229–231.
- Hall, M. D., L. F. Bussière, J. Hunt, and R. Brooks. 2008. Experimental evidence that sexual conflict influences the opportunity, form and intensity of sexual selection. *Evolution* 62:2305–2315.
- Hall, M. D., L. McLaren, R. C. Brooks, and S. P. Lailvaux. Interactions among performance capacities predict male combat outcomes in the field cricket *Teleogryllus commodus*. *Functional Ecology*, *in press*.
- Hansen, T. F., and D. K. Price. 1995. Good genes and old age: Do old males provide superior genes? *Journal of Evolutionary Biology* 8:759–778.
- Hine, E., and M. W. Blows. 2006. Determining the effective dimensionality of the genetic variance-covariance matrix. *Genetics* 173:1135–1144.
- Houle, D. 1991. Genetic covariance of fitness correlates: what genetic correlations are made of and why it matters. *Evolution* 45:630–648.
- Houle, D. 1992. Comparing evolvability and genetic variability of quantitative traits. *Genetics* 130:195–204.
- Hunt, J., R. Brooks, M. D. Jennions, M. J. Smith, C. L. Bentsen, and L. F. Bussière. 2004a. High-quality male field crickets invest heavily in sexual display but die young. *Nature* 432:1024–1027.
- Hunt, J., L. F. Bussière, M. D. Jennions, and R. Brooks. 2004b. What is genetic quality? *Trends in Ecology and Evolution* 19:329–333.
- Hunt, J., M. D. Jennions, N. Spyrou, and R. Brooks. 2006. Artificial selection on male longevity influences age-depen-

- dent reproductive effort in the black field cricket *Teleogryllus commodus*. *American Naturalist* 168:E72–E86.
- Husak, J. F., and S. F. Fox. 2008. Sexual selection on locomotor performance. *Evolutionary Ecology Research* 10:213–228.
- Husak, J. F., S. F. Fox, M. B. Lovern, and R. A. Van Den Bussche. 2006. Faster lizards sire more offspring: Sexual selection on whole-animal performance. *Evolution* 60:2122–2130.
- Husak, J. F., S. F. Fox, and R. A. Van Den Bussche. 2008. Faster male lizards are better defenders not sneakers. *Animal Behaviour* 75:1725–1730.
- Husak, J. F., A. K. Lappin, and R. A. Van Den Bussche. 2009. The fitness advantage of a high-performance weapon. *Biological Journal of the Linnean Society* 96:840–845.
- Huyghe, K., B. Vanhooydonck, H. Scheers, M. Molina-Borja, and R. Van Damme. 2005. Morphology, performance and fighting capacity in male lizards, *Gallotia galloti*. *Functional Ecology* 19:800–807.
- Irschick, D., J. K. Bailey, J. A. Schweitzer, J. F. Husak, and J. J. Meyers. 2007a. New directions for studying selection in nature: studies of performance and communities. *Physiological and Biochemical Zoology* 80:557–567.
- Irschick, D. J., and T. J. Garland. 2001. Integrating function and ecology in studies of adaptation: investigations of locomotor capacity as a model system. *Annual Reviews in Ecology and Systematics* 32:367–396.
- Irschick, D. J., A. Herrel, B. Vanhooydonck, and R. Van Damme. 2007b. A functional approach to sexual selection. *Functional Ecology* 21:621–626.
- Irschick, D. J., J. J. Meyers, J. F. Husak, and J. Le Galliard. 2008. How does selection operate on whole-organism functional performance capacities? A review and synthesis. *Evolutionary Ecology Research* 10:177–196.
- Kachigan, S. K. 1991. *Multivariate statistical analysis: a conceptual introduction*. Second edition. Radius Press, New York, New York, USA.
- Kirkpatrick, M. 1996. Good genes and direct selection in the evolution of mating preferences. *Evolution* 50:2125–2140.
- Kirkpatrick, M., and N. H. Barton. 1997. The strength of indirect selection on female mating preferences. *Proceedings of the National Academy of Sciences (USA)* 94:1282–1286.
- Kirkpatrick, M., and M. J. Ryan. 1991. The evolution of mating preferences and the paradox of the lek. *Nature* 350:33–38.
- Kokko, H. 1997. Evolutionarily stable strategies of age-dependent sexual advertisement. *Behavioral Ecology and Sociobiology* 41:99–107.
- Kokko, H. 1998. Good genes, old age and life-history trade-offs. *Evolutionary Ecology* 12:739–750.
- Kokko, H., R. Brooks, M. D. Jennions, and J. Morley. 2003. The evolution of mate choice and mating biases. *Proceedings of the Royal Society B* 270:653–664.
- Kokko, H., M. D. Jennions, and R. Brooks. 2006. Unifying and testing models of sexual selection. *Annual Review of Ecology and Systematics* 37:43–66.
- Lailvaux, S. P., A. Herrel, B. Vanhooydonck, J. J. Meyers, and D. J. Irschick. 2004. Performance capacity, fighting tactics and the evolution of life-stage male morphs in the green anole lizard (*Anolis carolinensis*). *Proceedings of the Royal Society B* 271:2501–2508.
- Lailvaux, S. P., and D. J. Irschick. 2006a. A functional perspective on sexual selection: insights and future prospects. *Animal Behaviour* 72:263–273.
- Lailvaux, S. P., and D. J. Irschick. 2006b. No evidence for female association with high-performance males in the green anole lizard, *Anolis carolinensis*. *Ethology* 112:707–715.
- Lailvaux, S. P., and D. J. Irschick. 2007. The evolution of performance-based male fighting ability in Caribbean *Anolis* lizards. *The American Naturalist* 170:573–586.
- Lappin, A. K., and J. F. Husak. 2005. Weapon performance, not size, determines mating success and potential reproductive output in the collared lizard (*Crotaphytus collaris*). *American Naturalist* 166:426–436.
- Losos, J. B., D. A. Creer, and J. A. Schulte. 2002. Cautionary comments on the measurement of maximum locomotor capabilities. *Journal of Zoology* 258:57–61.
- Marsh, R. L., and H. B. John-Alder. 1994. Jumping performance of hylid frogs measured with high-speed cine film. *Journal of Experimental Biology* 188:131–141.
- Nicoletto, P. F. 1991. The relationship between male ornamentation and swimming performance in the guppy, *Poecilia reticulata*. *Behavioral Ecology and Sociobiology* 28:365–370.
- Nicoletto, P. F. 1993. Female sexual response to condition-dependent ornaments in the guppy, *Poecilia reticulata*. *Animal Behaviour* 46:441–450.
- Roff, D. A., and D. J. Fairbairn. 2007. The evolution and genetics of migration in insects. *BioScience* 57:155–164.
- Rowe, L., and D. Houle. 1996. The lek paradox and the capture of genetic variance by condition dependent traits. *Proceedings of the Royal Society B* 263:1415–1421.
- Royle, N. J., N. B. Metcalfe, and J. Lindstrom. 2006. Sexual selection, growth compensation and fast-start swimming performance in green swordtails, *Xiphophorus helleri*. *Functional Ecology* 20:662–669.
- Saxton, A. M., editor. 2004. *Genetic analysis of complex traits using SAS*. Books By Users Press, Cary, North Carolina, USA.
- Shackleton, M. A., M. D. Jennions, and J. Hunt. 2005a. Fighting success and attractiveness as predictors of male mating success in the black field cricket, *Teleogryllus commodus*: the effectiveness of no-choice tests. *Behavioral Ecology and Sociobiology* 58:1–8.
- Shackleton, M. A., M. D. Jennions, and J. Hunt. 2005b. Fighting success and attractiveness as predictors of male mating success in the black field cricket, *Teleogryllus commodus*: the effectiveness of no-choice tests. *Behavioral Ecology and Sociobiology* 58:1–8.
- Snowberg, L. K., and C. W. Benkman. 2009. Mate choice based on a key ecological performance trait. *Journal of Evolutionary Biology* 22:762–769.
- Takahashi, D., and M. Kohda. 2004. Courtship in fast water current by a male stream goby (*Rhinogobius brunneus*) communicates the parental quality honestly. *Behavioral Ecology and Sociobiology* 55:431–438.
- Toro, E., A. Herrel, and D. J. Irschick. 2004. The evolution of jumping performance in Caribbean *Anolis* lizards: solutions to biomechanical trade-offs. *American Naturalist* 163:844–856.
- Toro, E., A. Herrel, B. Vanhooydonck, and D. J. Irschick. 2003. A biomechanical analysis of intra- and inter-specific scaling of jumping and morphology in Caribbean *Anolis* lizards. *Journal of Experimental Biology* 206:2641–2652.
- Vanhooydonck, B., P. Aerts, D. J. Irschick, and A. Herrel. 2006. Power generation during locomotion in *Anolis* lizards: an ecomorphological approach Pages 253–269 in A. Herrel, T. Speck, and N. Rowe, editors. *Ecology and Biomechanics: A mechanical approach to the ecology of animals and plants*. CRC Press, Boca Raton, Florida, USA.
- Veasey, J. S., D. C. Houston, and N. B. Metcalfe. 2001. A hidden cost of reproduction: the trade-off between clutch size and escape take-off speed in female zebra finches. *Journal of Animal Ecology* 70:20–24.
- Winter, D. A. 2005. *Biomechanics and motor control of human movement*. Third edition. Wiley, Hoboken, New Jersey, USA.
- Zahavi, A. 1975. Mate selection: a selection for a handicap. *Journal of Theoretical Biology* 53:205–214.
- Zajitschek, F., J. Hunt, S. R. Zajitschek, M. D. Jennions, and R. Brooks. 2007. No intra-locus sexual conflict over reproductive fitness or ageing in field crickets. *PLoS ONE* 2:e155.