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DIFFERENTIAL AGING OF BITE AND JUMP PERFORMANCE IN VIRGIN AND MATED *TELEOGRYLLUS COMMODUS* CRICKETS

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Evolutionary theories of aging state that the force of natural selection declines with age, resulting in trait senescence. However, sexual selection theory predicts that costly traits that signal mate value should increase in expression as survival prospects decline. Mortality rates and fertility tend to show strong signatures of senescence, whereas sexual signaling traits increase with age, but how the expression of traits such as whole-organism performance measures that are subject to both sexual and nonsexual selection should change with age is unclear. We examined the effects of both a key life-history event (mating) and diet quality (male and female optimal diets) on aging in two whole-organism performance traits (bite force and jump take-off velocity) in male and female *Teleogryllus commodus* crickets. We found no evidence for diet effects on any of the measured traits. Aging effects were more evident in females than in males for both jumping and biting, and constitute a mix of senescence and terminal investment patterns depending on sex/mating class. Sex and mating therefore have important implications for resource allocation to performance traits, and hence for aging of those traits, and interactions between these two factors can result in complex changes in trait expression over individual lifetimes.

KEY WORDS: Aging, diet, life-history, whole-organism performance.

The evolutionary theory of aging hinges on the fundamental idea that the force of natural selection declines as individuals age (Medawar 1952; Williams 1957; Charlesworth 1994; Hughes and Reynolds 2005). Fitness traits often senesce because early-life performance is typically far more important for fitness than is performance in late adulthood (Stearns et al. 2000; Williams et al. 2006). However, senescence is not the only possible age-dependent pattern of fitness trait expression. Indeed, life-history theory predicts that investment in both reproductive effort and traits closely tied to reproduction should often increase with age as survival prospects decline (Williams 1966; Kokko 1997, 1998). In both cases, age-dependence is expected to be mediated by diet and condition. Consequently, diet composition, as well as the timing of key life-history events that might strongly influence resource allocation toward a particular trait or suite of traits, may be important factors affecting the rate and direction of age-related changes in trait expression.

The allocation of limited, acquired, resources to various functions lies at the heart of life-history theory (Stearns 1989; Houle 1991). The acquisition of resources and their allocation to reproductive effort, somatic maintenance (and thus survival prospects), and ecological performance are tightly interconnected (Ghalambor et al. 2003, 2004). Experimental and evolutionary gerontology has provided ample evidence of the complex relationships between diet, reproductive effort, and longevity (Williams 1957, 1966; Partridge and Barton 1993). But allocation of resources to reproduction may also affect other important physiological traits, such as whole-organism performance capacities (defined as any measure of an organism conducting a dynamic, ecologically relevant task such as running or biting; see Bennett and Huey 1990; Irschick and Garland 2001; Lailvaux and Irschick 2006 for discussion). Performance traits may be related to fitness through different pathways—locomotor performance, for example, may be important for predator escape, or mate acquisition, or both (Husak and Fox 2008). Furthermore, the form of either type of selection may change over individual lifetimes. In *Crotaphytus collaris* lizards, for example, selection analyses show that sprint speed predicts survival in hatchlings and not at all in adults (Husak 2006), but does predict adult male reproductive success (Husak et al. 2006), likely through enhanced female defense by faster males (Husak et al. 2008). Divergent selection pressures over individual lifetimes may therefore affect the aging of such traits in different ways, but the cumulative effect of different selective contexts on the aging of such traits, particularly when mediated by diet, has not been explored.

Age-dependent declines in locomotor activity have been demonstrated previously in several species, including dogs (Siwak et al. 2002) and humans (e.g., Rittweger et al. 2009 and references therein; Bernard et al. 2010), typically from the perspectives of biomechanics or kinematics. By contrast, the role of aging and potential senescence on performance traits within an evolutionary or life-history context has received less attention. Indeed, although previous studies have shown that juvenile animals may use a relatively greater percentage of their maximum performance capacities than adults (Carrier 1996; Irschick 2000; Dangles et al. 2007), the life-history of performance over adult lifetimes is seldom considered. Trade-offs between adult performance and reproduction, in particular, could strongly influence survival and fitness (Ghalambor et al. 2003, 2004). For example, Veasey et al. (2001) demonstrated a reduction in flight take-off speed following egg-laying (independent of the weight of the eggs) in adult female zebra finches (*Taeniopygia guttata*), suggesting a key trade-off between fecundity and somatic maintenance related to flight. Given the demonstrated links between performance and survival (reviewed in Irschick et al. 2007, 2008), compromised locomotor ability may therefore ultimately curtail individual life spans. However, Reznick et al. (2004)showed that increased predation led to earlier onset of senescence in fast-start performance but not in mortality or reproduction in guppies. Thus, performance may show aging patterns that differ from those in other life-history traits, depending on their association with reproduction and lifetime reproductive success. In addition, those patterns may also differ among performance traits depending on the nature of the performance->fitness relationships for each trait.

Although reproductive investment may affect the expression of performance traits, the nature and timing of reproductive investments by males and females are, in most species, quite different, as are the relationships between performance and fitness (Calsbeek and Irschick 2007; Irschick et al. 2008). It follows that males and females should often differ in their diet- and age-dependent reproductive effort and performance (Bonduriansky et al. 2008). The costs of reproductive effort and the fact that performance capacities influence both reproductive success and survival (reviews in Lailvaux and Irschick 2006; Husak and Fox 2008; Irschick et al. 2008) mean that males and females might follow very different age trajectories in performance traits, and that those traits might respond differently to diet manipulations. Consequently, it is of interest to understand the effects of diet in conjunction with key life-history events such as mating, which may alter resource allocation, and hence patterns of aging, on male and female performance traits. Indeed, mating status and mating regimes have been repeatedly shown to have important (and often sex-specific) effects on aging and longevity in a variety of animal species (e.g., Aigaki and Ohba 1984; Paukku and Kotiaho 2005; Stolz et al. 2010). Given the general importance of whole-organism performance to a variety of ecological tasks in numerous selective contexts, ranging from mate and/or territory acquisition and defense (Husak et al. 2006, 2008; Hall et al. 2010b) to escape behavior (Lailvaux et al. 2003; Irschick et al. 2005; Dangles et al. 2007), dispersal (Phillips et al. 2006), and feeding (Vincent et al. 2005; Herrel et al. 2001, 2006), an understanding of the life-history factors affecting performance traits in males and females over individual lifetimes is essential to understanding both the ecology and evolution of performance traits.

In this study, we examine aging in two whole-organism performance traits (maximum jumping ability and maximum bite performance) in both virgin and mated adult male and female *Teleogryllus commodus* crickets. Individuals were raised on two different diet treatments (one close to the fitness optimum for males, the other close to the optimum for females) that have previously been shown to maximize sex-specific reproductive investment in this species (Maklakov et al. 2008, 2009). By manipulating a factor that affects reproductive investment differently in males and females, we are likely to affect aging in traits related to reproduction as well. *Teleogryllus commodus* is an ideal species for a study of this type, given both the existing body of knowledge investigating reproductive investment, trade-offs, and aging in this species, as well as more recent work considering the ecology and evolution of cricket performance. Jumping performance might be expected to be largely exempt from aging effects in crickets given that jumping is driven largely by an elastic energy-storage mechanism in these and related animals (Bennet-Clark 1975; Burrows and Morris 2003; Hustert and

Baldus 2010). However, a recent study using *T. commodus* showed that jumping is negatively genetically correlated with calling effort (Lailvaux et al. 2010) hinting at a potential life-history trade-off between these two variables and strongly suggesting that females who choose to mate with males based on calling effort will be choosing males who have low breeding values for jumping performance. Jumping performance also both decreases over the course of ontogeny and improves predator escape in other cricket species (Dangles et al. 2007). It therefore appears likely that the evolution of male jump performance via predator-induced selection may be opposed by indirect sexual selection via the negative genetic covariance with calling effort, and that jump performance may change with age in adult crickets as well. In contrast to jump performance, bite force predicts success in male combat outcomes in a variety of taxa (Lailvaux et al. 2004; Huyghe et al. 2005; Lailvaux and Irschick 2007), including *T. commodus* (Hall et al. 2010b). Bite force is therefore a performance trait under consistent positive sexual selection in males. We test the hypothesis that mating status, in conjunction with diet, will affect the aging of both performance traits in *T. commodus*. Specifically, we predict that (1) jump performance will exhibit senescence in unmated males on male-optimal diets, given the known trade-offs between calling effort (and hence attractiveness) and longevity (Hunt et al. 2004), and between attractiveness and jump performance in this species (Lailvaux et al. 2010). By contrast, unmated males on female-optimal diets might be expected to maintain allocation toward jump performance due to lower investment in calling, and hence jumping may senescence less than males on male-optimal diets; (2) bite force will senesce in unmated females but may stay constant or even increase in unmated males with age due to the importance of bite force to male combat; (3) both jump performance and bite force will decline in mated males and females as a result of the costs associated with reproduction.

Methods

EXPERIMENTAL DESIGN

We used a 2 × 2 × 2 design, in which we manipulated diet (two levels) and mating status (two levels) in males and females, resulting in eight treatments: diet A/virgin, diet A/mated, diet B/virgin, diet B/mated for each sex. We manipulated resource acquisition by providing experimental crickets with one of two artificial diets: a diet (A) that is close to the diet composition known to maximize lifetime calling effort of virgin males, and a diet (B) that maximizes female lifetime fecundity (Maklakov et al. 2008). Diet A had a 1:8 protein:carbohydrate ratio (9.33% protein and 74.66% carbohydrate), diet B had a 1:1 P:C ratio (42% protein and 42% carbohydrate). Mating status was defined as either virgin (V; unmated) or mated (M). An "M" cricket was mated overnight with a random stock culture individual of the opposite sex every seven days until it died. On the day of eclosion into adulthood, we isolated experimental crickets from laboratory stock cultures (originally from Smith's Lake, NSW, Australia), fed a diet of cat food (Friskies Go-Cat Senior, Nestlé Australia, Sydney Australia) and water. Crickets were kept from eclosion date until they died in individual plastic containers (5 × 5 × 5 cm) that contained a piece of egg carton for shelter and a plastic water bottle plugged with cotton wool. We assigned individuals of each sex randomly to one of the four treatments. On the day of eclosion (adult age = 0 days), we measured pronotum width using an eyepiece graticule in a Leica MZ5 binocular microscope (Leica Microsystems, North Ryde, Australia), and weighed each cricket on an electronic balance (Mettler-Toledo, model AG135, Mettler-Toledo Ltd, Port Melbourne, Australia) to the nearest 0.0001 g. We cleaned plastic containers, and provided each individual with new diet and water weekly. We checked all animals daily for survival.

Four hundred hatchling *T. commodus* were assigned to one of eight treatment/sex groups at the beginning of the experiment. At birth, we also randomly assigned an age of performance measurement to each individual, with a range of ages starting at seven days of adult age, every seven days, up until age 70 days. Thus, performance measures in all experimental males and females were taken only once for each individual. Because a number of individuals died before their assigned measuring dates (individual life spans ranged from 2 to 119 days posteclosion) our overall sample size is smaller than the 400 individuals we started with. Similarly, because not all individuals could be measured for both traits (e.g., several crickets lost one or more legs prior to jump measurement), sample sizes for performance traits are unequal. Specific sample sizes for the various diet (A or B), mating (M or V), and sex (M or F) combinations for bite force were: AMF = 8, BMF = 20, AVF = 13, BVF = 22, AMM = 17, BMM = 23, AVM = 20, BVM = 27. For jumping, the sample sizes were as follows: AMF = 21, BMF = 31, AVF = 24, BVF = 25, AMM = 28, BMM = 34, AVM = 31, BVM = 32. (Note, however, that due to lack of any significant diet effect, diet treatments were ultimately pooled for aging analyses [see below]).

BITE FORCE

We measured bite force using the same methods as in Hall et al. (2010b). Briefly, we placed a Tekscan FlexiForce Wireless ELF system (Tekscan Inc., Boston, MA) force circuit between each crickets' mandibles, invariably causing the crickets to bite down aggressively. We measured bite force five times per individual (Adolph and Pickering 2008) and retained the maximum measured bite force for each individual for analysis (see Losos et al. 2002 for justification of the use of maximal values in performance studies).

JUMP PERFORMANCE

To measure jump performance in *T. commodus*, we used a Fastec high-speed camera (Fastec Imaging, San Diego, CA) with a frame rate of 500 fps to capture video clips of crickets jumping unassisted off of a designated jump platform (following Hall et al. [2010b]; Lailvaux et al. [2010]). We placed a mirror at a 45° angle above the jump platform that allowed us to film both dorsal and lateral views simultaneously. We later merged these two jump trajectories into a single three-dimensional view of each jump using Pythagoras's rule. We taped a 1 × 1 cm grid behind the jump platform for scale. As for bite force, we jumped each individual at least five times and retained the best jumps for analysis (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 version 1.5.1.9 (Xcitex Inc., Cambridge, MA). We digitized only the center of the head during each jump, given that there was little or no rotation of the head in most jumps (Marsh and John-Alder 1994). We began digitizing 20 frames before the first movement, and stopped when the cricket either hit a wall or left the frame. We smoothed the x, y, and z measurements thus obtained using a zero phase-shift Butterworth filter (Winter 2005) and calculated instantaneous velocity from the smoothed displacements.

STATISTICAL ANALYSIS

To examine the effects of diet and mating status and sex on whole-organism performance independent of aging effects, we used separate three-way general linear models (GLMs) for bite force and jump performance. To explicitly model the effects of aging on performance traits, we included linear and quadratic age terms in a second set of models. We initially fitted "saturated" models including all possible two-way interactions, and employed model simplification techniques to arrive at the minimum adequate model exhibiting the lowest Akaike information criteria (AIC). To visualize the curvilinear effects of age and categorical effects of diet and sex on each performance trait, we plotted smoothed curves derived from best-fitting general additive models (GAM). We used takeoff velocity in all analyses as a proxy for jump performance, although we note that our results are qualitatively very similar if we use other measures of jump performance. All analyses were conducted using R 2.9.2.

Results

We found no evidence for a diet effect on bite force or jump performance, either alone or in conjunction with other factors (Fig. 1). Consequently, diets were pooled for all subsequent analyses. Cricket weight at eclosion differed significantly between sexes, with males being heavier than females ($F_{1,567} = 27.1267$, $P < 0.001$) (Fig. 2).

The three-way GLMs showed significant effects of mating and sex on bite force, as well as a marginally nonsignificant interaction between mating and sex (Table 1). The model that best described the variation in bite force over adult lifetimes contained linear, quadratic and cross-product terms (AIC = 258.17, no. of parameters = 7; Table 2). The model containing only linear terms was the next best (AIC = 269.74, no. of parameters = 4), but showed a substantially worse fit than the best-fitting model (ΔAIC = 11.57; Burnham and Anderson 2002). (Note that because weight was retained in the best-fitting models for both bite [Table 2] and jump performance [Table 3], these traits are interpreted as being corrected for body weight). The interactions between the sex term and mating and age, respectively, indicate that mated and virgin males and females tend to exhibit different weight-corrected aging curves (Figs. 3 and 4). Specifically, female bite forces tend to increase with age in both mating treatments after weight has been accounted for, with the exception of a marked drop in bite force for older mated females. By contrast, weight-corrected bite force shows relatively little change in magnitude over individual mated male life spans, exhibiting a shallow increase with age (although note that the confidence intervals for this curve are fairly wide) (Fig. 3). However, a gradual decrease in maximum bite force can be perceived in virgin male crickets from approximately 40 days onward.

The three-way GLMs showed no significant effects of mating, diet, or sex on takeoff velocity on *T. commodus* (Table 1). Linear and cross-product terms were retained within the GLM that best described variation in takeoff velocity over individual lifetimes (AIC = 182.12, no. of parameters = 5; Table 3). The next best model included linear, quadratic, and cross-product terms (AIC = 183.93, no. of parameters = 8), whereas the model containing only linear terms was the least informative (AIC = 188.65, no. of parameters = 4). The age effect is manifest as a marked decline in weight-corrected takeoff velocity with increasing age, particularly in females, although jump performance in males from both mating treatments remains remarkably constant across individual lifetimes following correction for body weight (Fig. 4).

Discussion

DIET DOES NOT AFFECT PERFORMANCE TRADE-OFFS DURING AGING

Patterns of aging can be affected by trade-offs among life-history traits, and may differ between the sexes if male and female allocation patterns also differ (Bonduriansky et al. 2008). We tested several predictions regarding the effects of diet and mating status on aging of two whole-organism performance traits in *T. commodus* crickets. We found no effect of the considered diets on performance, either alone or in interaction with other treatment factors (Table 1; Figs. 1 and 2). This result contrasts with the

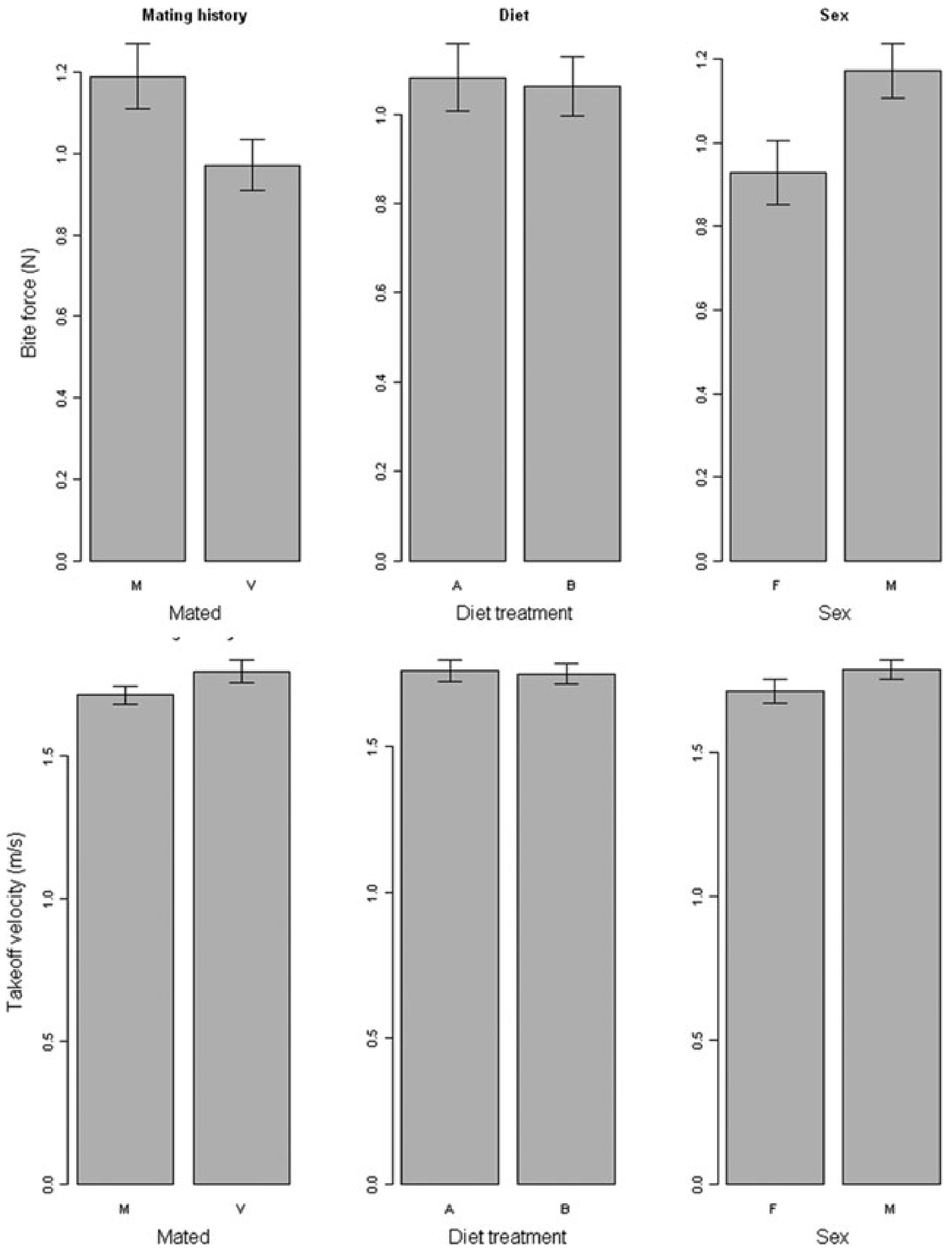

Figure 1. **Effects of mating treatment, diet, and sex on (A) maximum bite force, and (B) maximum takeoff velocity in *T. commodus* crickets. Columns represent means, calculated over all ages. Error bars represent ± 1 SE.**

documented effects of these same diets on reproductive investment in *T. commodus* (Maklakov et al. 2008), as well as diet effects on reproductive aging in this species (Maklakov et al. 2009). Thus, although our diet treatments used in this study clearly affect reproductive investment and reproductive aging in *T. commodus*, they appear to have little influence on either of the measured whole-organism performance traits (Table 1) or on the aging of those traits (Tables 2 and 3). Our prediction regarding an effect of male diet on jump senescence was therefore not supported, and our diet treatment does not appear to affect the expression or aging of either performance trait, either alone or in conjunction with sex or mating.

Effects of diet on performance have been considered in relatively few species, and hence it is difficult to place our results in a comparative context. Although similar studies using sex-optimized diets are not available, simple dietary restriction

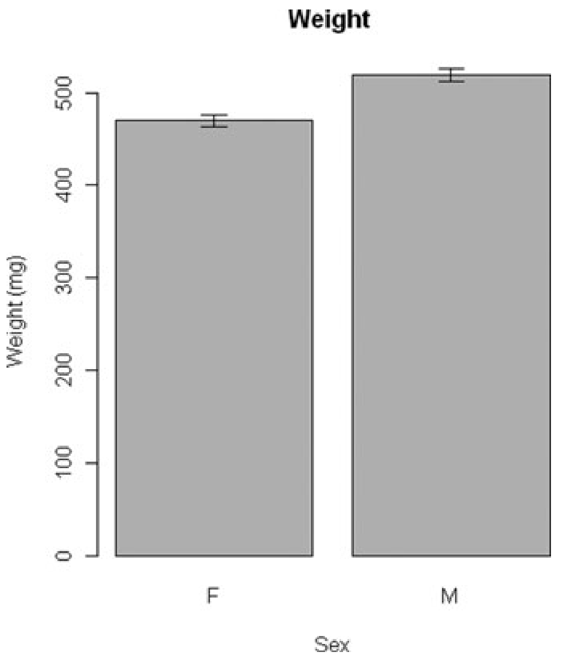

Figure 2. Weight at eclosion into adulthood in male and female *T. commodus.*

Table 2. Parameter estimates of the best-fitting model describing the variation in bite force over individual lifetimes.

Traits	Estimate	SE	t	P-value
Mating	−0.008	0.141	−0.06	0.952
Sex	0.784	0.221	3.544	<0.001
Age	0.044	0.012	3.760	<0.001
Weight	<0.001	<0.001	1.574	0.117
Age^2	<0.001	<0.001	−2.536	0.012
Sex×age	−0.016	0.006	−2.721	0.007

during development has been shown to negatively affect swimming endurance (Royle et al. 2006a), but not fast-start swimming performance (Royle et al. 2006b) in adult *Xiphophorus helleri* fish. Le Galliard et al. (2004) found an interaction between diet and endurance in juvenile *Lacerta vivipera* lizards such that fully fed individuals exhibited significant stabilizing change in endurance (i.e., those with relatively poor endurance catch up, whereas those with an endurance advantage decline) relative to those on restricted diets, whereas dietary restriction during development was found to negatively affect maximum bite force in adult male *Anolis carolinensis* lizards (R. Gilbert, J. Edwards, and S. P. Lailvaux, unpubl. data). Given that these studies collectively point toward potentially important effects of diet on whole-organism performance in general, the lack of any effect of the considered diets in this experiment is surprising. This is especially so considering the large differences between the two diets in terms of protein content (i.e., 9.3% vs. 42%), which might be expected to affect muscle growth and maintenance. Future studies considering the effects of a wider range of diets on whole-organism performance capacities would be valuable for understanding this important life-history factor.

MATING EFFECTS ON THE AGING OF WHOLE-ORGANISM PERFORMANCE

Mating has previously been shown to be a costly and important life-history event that can affect resource allocation and utilization in a variety of animal species. We therefore predicted that mated males and females would exhibit declines in both measured performance variables as a result of these costs. Previously, Goto and Higuchi(2004) showed that tethered flight performance differed little between mated and unmated *Trigonotylus caelestialium* rice leaf bugs regardless of sex over a relatively short age duration (three- to five-day old). By contrast, we found that mating status had a clear effect on both overall female bite force (Table 1) and on the aging of both bite force (Table 2) and jumping ability (Table 3) in *T. commodus*, regardless of the diet treatment. Maximum bite force peaks between 30 and 40 days of age and then declines in mated females and virgin males, whereas it increases throughout adulthood in virgin females and shows an arguable

Table 1. Results of three-way GLMs describing the effects of diet type, mating treatment, and sex on bite force and takeoff velocity in *T. commodus*. (Note that these results are qualitatively similar if weight is included as a covariate).

Bite force				Takeoff velocity		
Variable	df	F	P-value	df	F	P-value
Diet	1,142	0.041	0.952	1,218	0.042	0.84
Mating	1,142	5,081	<0.026	1,218	2.63	0.11
Sex	1,142	5.927	<0.016	1,218	2.06	0.15
Diet×Mating	1,142	0.025	0.88	1,218	0.28	0.60
Diet×Sex	1,142	0.001	0.99	1,218	0.12	0.73
Mating×Sex	1,142	3.68	0.057	1,218	0.012	0.91
Diet×Mating×Sex	1,142	1.91	0.17	1,218	0.062	0.80

Table 3. Parameter estimates of the best-fitting model describing the variation in takeoff velocity over individual lifetimes.

Traits	Estimate	SE	*t*	*P*-value
Mating	0.092	0.133	12.442	<0.001
Sex	−0.169	0.965	−1.949	0.053
Age	−0.01	0.002	−4.533	<0.001
Weight	<0.001	<0.001	2.763	0.006
Sex×Age	0.009	0.003	2.908	0.004

slight increase in mated males (Fig. 3). Thus, our prediction that bite force should senesce in all mated animals regardless of sex is only partially supported, as no obvious decline in bite force was seen for mated males. We also predicted that unmated rather than mated males would show age-dependent increases in bite force (as predicted by sexual selection theory), but in fact the opposite was true. Most surprisingly, we document a pattern again entirely opposite to that predicted for bite force of unmated females, with maximum bite force clearly and steadily increasing. Such an increase in bite force over time is consistent with terminal investment, whereby individuals increase resource investment in a given trait as survival prospects decline. This steady increase in bite force in virgin females is curious; however, we currently know nothing about the ecological significance of bite force in female crickets. One possibility is that females allocate resources toward bite force as a form of mating resistance, given that male harassment imposes strong direct and indirect costs on females (Hall et al. 2008, 2010a). It is unclear, however, why resistance would increase in unmated females that are not subject to harassment (Arnqvist and Rowe 2005). A further possibility is that bite force is a correlate of other physiological capabilities that we have not yet measured. The rise and then fall in mated female bite force may indicate age-dependent increase in reproductive effort, coupled with senescence as a cost of mating; future research on the role of bite force in females and on the physiological correlates of bite force might shed light on the curious patterns we document in female bite force.

The interaction between mating status and sex was only marginally nonsignificant for bite force (Table 1), suggesting that mating may affect bite force expression differently in males and females. Indeed, males exhibit much higher absolute bite forces than females (Fig. 1; although this pattern seems to be largely driven by mated males, see Fig. 3), as expected in a trait known to be important in determining male combat outcomes (see Lailvaux and Irschick 2007). For example, Hall et al. (2010b) showed that bite force predicts male combat outcomes in *T. commodus*, (both alone and in combination with other predictors), and Judge and Bonanno (2008) found evidence that head size (which is

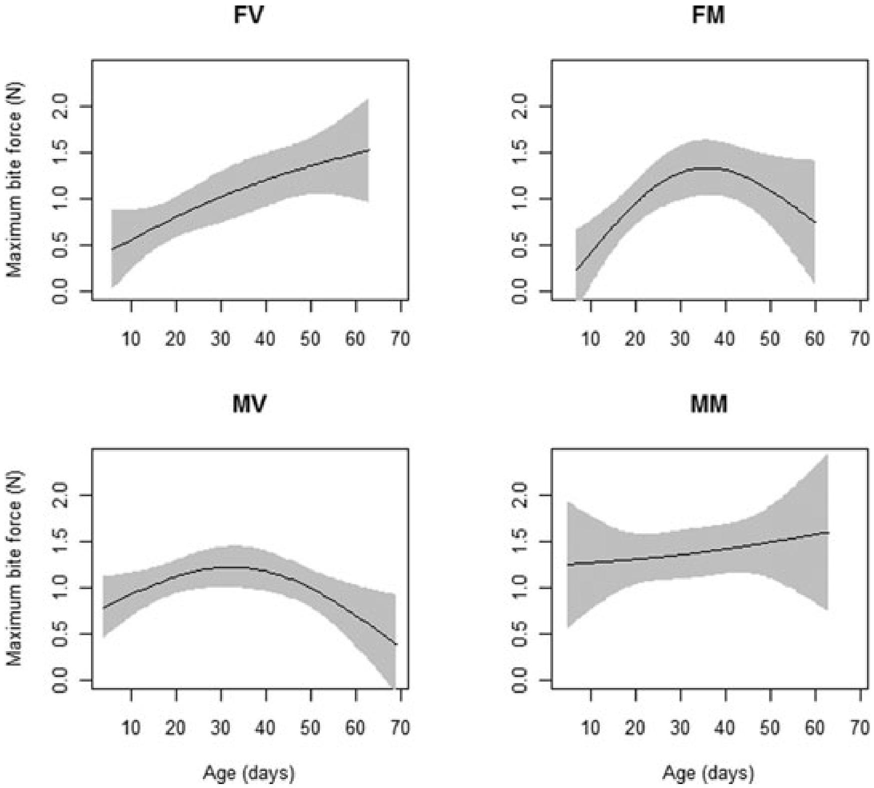

Figure 3. Relationships between maximum bite force and age in all combinations of sex/mating treatments. Gray areas are 95% confidence intervals.

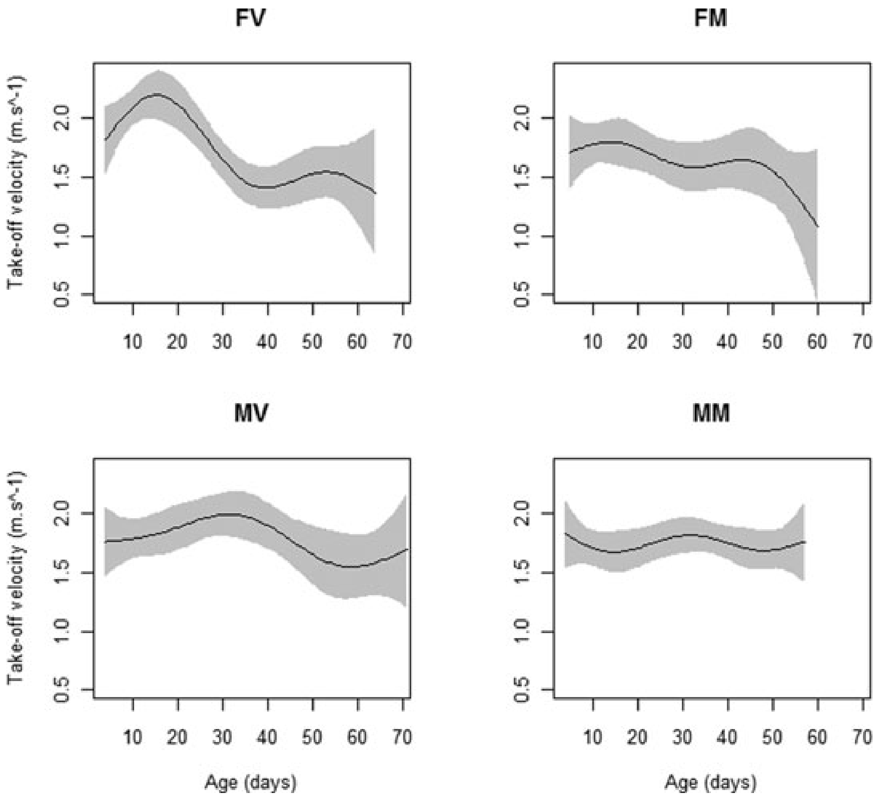

Figure 4. Relationships between maximum takeoff velocity and age in all combinations of sex/mating treatments. Gray areas are 95% confidence intervals.

functionally correlated with bite force in a variety of animal species; Herrel et al. 2007; Anderson et al. 2008; Huyghe et al. 2009) is under positive selection through male–male combat in *Gryllus pennsilvanicus* crickets. Males with larger heads and higher bite forces also tend to win fights more frequently in house crickets, *Acheta domesticus* (C. Condon and S. P. Lailvaux, unpubl. data). Our findings that male bite force changed relatively little with age regardless of mating treatment suggests that bite force is prioritized in males—-perhaps because it is an especially important trait at all ages. As another potentially important consideration, adult males and females differ not only in bite force, but also in the thickness of consumed foliage in another orthopteran species, *Romalea microptera* (Vincent 2006). If *T. commodus* males and females partition diet resources in nature in a similar manner, or alternatively shift their diet preferences as they age, then feeding ecology may contribute to the observed differences in bite force aging as well.

In contrast to bite force, and again contrary to our predictions, jump performance declines markedly with age in female virgin *T. commodus*, and somewhat less so in mated females. Male jump performance, on the other hand, remains constant over time in both mated and unmated individuals. Although the starkly different age-dependence patterns for bite force and jump performance in virgin females suggest that these two different performance traits may trade-off or at least not be strongly associated in females, this interpretation is counterintuitive given that costs of mating should be manifest as trade-offs in “mated” animals, rather than virgins (Arnqvist and Rowe 2005). Furthermore, there is no a priori reason to expect a positive relationship between size-corrected bite force and jump performance in the absence of resource allocation, and hence the pattern exhibited may not necessarily reflect adaptive allocation (Stearns 1989). The lack of an explicit aging effect in male jump performance in either mating treatment is consistent with the weak effects of age on male bite force, but somewhat unexpected from a life-history perspective given the costly nature of both male advertisement and mating. It is also of interest given the known links between locomotion and natural selection in a variety of animals, including crickets (Le Galliard et al. 2004; Walker et al. 2005; Calsbeek and Irschick 2007; Dangles et al. 2007). For example, Zajitscheck et al. (2009) showed that wild male *T. commodus* exhibit higher mortality rates than females, possibly because extrinsic mortality is higher for males. One possibility, then, is that male crickets compensate for a higher baseline mortality rate by buffering jump performance against senescence (Zajitschek et al. 2009). Alternatively, the lack of an aging effect on jumping might be considered to be the "normal" state of affairs based on biomechanical considerations alone, and in particular the existence of an elastic loading mechanism for increasing jump performance in crickets.

CONCLUSIONS

In conclusion, our results clearly show that age-dependent whole-organism performance is affected by life-history trade-offs, and that these responses differ based on sex and mating treatment, but do not appear to be mediated by the male- and female-optimal diets considered here. Furthermore, these effects are trait-dependent, with bite force overall tending to be more plastic than jump performance. This differential effect of aging on different performance traits has important implications for our understanding of the ecology of whole-organism performance over individual lifetimes, and adds to a growing body of literature demonstrating both the necessity and the value of considering whole-organism performance within an explicit life-history framework (e.g., Ghalambor et al. 2003; Royle et al. 2006a; Lailvaux et al. 2010). Most strikingly, our results show evidence of complex interactions between sexual selection and nonsexual forms of natural selection on the measured performance traits in both sexes, and consequently we observed a mixture of sexually selected terminal investment and senescent aging patterns in both measured performance traits, the nature and causes of which are not immediately apparent from the current dataset. The sex-specific nature of our findings also lends further support for recent calls for increased focus on general sex-differences in functional and whole-organism performance traits (Huey and Pianka 2007; Lailvaux 2007).

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