

RESEARCH ARTICLE

Aerobic capacity in wild satin bowerbirds: repeatability and effects of age, sex and condition

Mark A. Chappell^{1,*}, Jean-Francois Savard², Jennifer Siani^{2,5}, Seth W. Coleman^{2,3}, Jason Keagy^{2,4} and Gerald Borgia²

¹Biology Department, University of California, Riverside, CA 92521, USA, ²Department of Biology and Behavior, Ecology, Evolution and Systematics Program, University of Maryland, College Park, MD 20742, USA, ³Department of Biology, Gonzaga University, Spokane, WA 99258, USA, ⁴Department of Zoology, Michigan State University, 203 Natural Sciences, East Lansing, MI 48824, USA and ⁵US Fish and Wildlife Service, State College, PA 16801, USA

*Author for correspondence (chappell@ucr.edu)

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SUMMARY

Individual variation in aerobic capacity has been extensively studied, especially with respect to condition, maturity or pathogen infection, and to gain insights into mechanistic foundations of performance. However, its relationship to mate competition is less well understood, particularly for animals in natural habitats. We examined aerobic capacity [maximum rate of O₂ consumption ($\dot{V}_{O_{2,max}}$) in forced exercise] in wild satin bowerbirds, an Australian passerine with a non-resource based mating system and strong intermale sexual competition. We tested for repeatability of mass and $\dot{V}_{O_{2,max}}$, differences among age and sex classes, and effects of several condition indices. In adult males, we examined interactions between aerobic performance and bower ownership (required for male mating success). There was significant repeatability of mass and $\dot{V}_{O_{2,max}}$ within and between years, but between-year repeatability was lower than within-year repeatability. $\dot{V}_{O_{2,max}}$ varied with an overall scaling to mass^{0.791}, but most variance in $\dot{V}_{O_{2,max}}$ was not explained by mass. Indicators of condition (tarsus and wing length asymmetry, the ratio of tarsus length to mass) were not correlated to $\dot{V}_{O_{2,max}}$. Ectoparasite counts were weakly correlated to $\dot{V}_{O_{2,max}}$ across all age–sex classes but not within any class. Adult males, the cohort with the most intense levels of mating competition, had higher $\dot{V}_{O_{2,max}}$ than juvenile birds or adult females. However, there was no difference between the $\dot{V}_{O_{2,max}}$ of bower-owning males and that of males not known to hold bowers. Thus one major factor determining male reproductive success was not correlated to aerobic performance.

Key words: aerobic capacity, repeatability, oxygen consumption, body condition, satin bowerbird.

INTRODUCTION

Trait variation is fundamental to the concept of evolution by natural selection. In recent years there has been considerable interest among ecological and evolutionary physiologists about how whole-animal performance differs among individuals, populations, age and sex classes or social ranks, and how these differences might affect fitness. Much of this work has focused on aspects of locomotor ability or energy metabolism that are assumed to be important for survival (e.g. sprint speed or thermogenesis) (Huey and Dunham, 1987; Chappell and Bachman, 1994; Hayes and O'Connor, 1999; Kvist and Lindström, 2001). Related studies have examined aspects of reproductive investment (e.g. egg production) (Vézina and Williams, 2005) or used individual variation to gain insight into mechanistic foundations of whole-animal performance (e.g. Burness et al., 1998; Chappell et al., 1999; Hammond et al., 2000).

In addition to consequences for survival, individual variation in performance might also affect fitness in a context of sexual selection. In many mating systems, members of one sex (usually males) aggressively compete for mating opportunities, either by acquisition and defense of territory or other resources needed for reproduction, or directly through combat. Moreover, females are often selective in terms of prospective mates, and are expected to make mating decisions on the basis of the resources or investment in offspring a

male can provide, or – particularly in non-resource-based mating systems such as leks – on the basis of male genetic quality. In both forms of sexual competition, individual differences in performance traits might be crucial for reproductive success.

One aspect of whole-organism performance that might be essential for survival and valuable in intermale competition, and also might provide an honest indication of male quality, is aerobic capacity (the maximal rate of oxygen consumption). Aerobic capacity is a major determinant of an animal's ability to engage in sustained intense activity (Bennett and Ruben, 1979). Because aerobic power production is dependent on the coordinated and effective function of a wide range of organ systems (e.g. pulmonary, cardiovascular, musculoskeletal, neural), it is likely to be a useful indicator of health and vigor. Hence, to the degree that it is heritable (Garland and Bennett, 1990; Dohm et al., 1996; Henderson et al., 2002), it may also be a signal of genetic quality. Aerobic performance variation has been extensively studied by mechanistic and ecological physiologists, but its role in mating systems, and especially in relation to female choice, has rarely been explored (Chappell et al., 1997).

In addition to individual variation, a crucial question when considering possible selection on a trait is repeatability. Repeatability (consistency of individual performance over time) is generally

assumed to be a prerequisite for and the upper limit to heritability (but see Dohm, 2002), which is necessary for a trait to evolve in response to selection. The repeatability of locomotor traits and certain indices of sub-maximal metabolism have been documented in a number of studies (e.g. Huey and Dunham, 1987; Labocha et al., 2004; Rønning et al., 2005; Szafranska et al., 2007). However, there have been few examinations of the repeatability of maximal aerobic performance (Hayes and Chappell, 1990; Chappell et al., 1996; Evans and Rose, 2010), and even fewer in wild populations (Chappell et al., 1995). In particular, we are aware of no reports of the repeatability of aerobic capacity in natural populations of any bird species, despite the importance of exercise performance to avian biology. In part, this may be due to the flexibility of metabolic traits in response to environmental variation, which can confound repeatability studies.

A long-running study of a wild population of satin bowerbirds (*Ptilonorhynchus violaceus* Vieillot) provided an opportunity to investigate variation in aerobic capacity in a species with a non-resource-based mating system with intense intermale competition and strong female choice (Marshall, 1954; Borgia, 1985a; Borgia, 1985b). Satin bowerbirds are fruit and insect-eating passerines native to mesic forests and rainforest in eastern Australia. Adult males build ground-level stick bowers at which all courtship activity and mating occurs. Bowers are decorated with flowers, feathers, berries etc. (Marshall, 1954; Cooper and Forshaw, 1977) and these decorations are important in female choice and male mating success (Borgia, 1985b; Borgia et al., 1987; Coleman et al., 2004). Males compete by stealing decorations from other males (Borgia and Gore, 1986) and will destroy the bowers of neighbors (Borgia, 1985a). Male courtship behavior includes presentation of decorations and dancing displays accompanied by loud vocalizations (Vellenga, 1970; Cooper and Forshaw, 1977), and females prefer males that display at high intensity (Patricelli et al., 2002). Another indication of strong sexual competition is that not all adult males are successful at constructing, maintaining and defending bowers, and as a result, there is considerable variability in male mating success (Borgia, 1985b). Aerobic capacity could be important in many aspects of bowerbird mating behavior, especially those requiring sustained activity.

In this study we explored variation of aerobic capacity, measured as maximal rates of oxygen consumption during forced exercise, in freshly-captured wild satin bowerbirds. We looked for effects of body condition, sex and age, and examined repeatability within seasons and over intervals as long as two years. We were also interested in whether there was a relationship between aerobic performance and sexual selection and competition. We posited that if aerobic capacity is important for male mating success in intrasexual competition or for female choice, then it should be higher in adult males than in females or juveniles. Because male mating success is dependent on bower ownership, we also hypothesized that bower-holding males should have higher aerobic performance than males not known to own bowers – in other words, we expected that a crucial factor in male mating success should be related to variation in aerobic physiology.

MATERIALS AND METHODS

Study site and bird handling

This study was carried out in 2001, 2002 and 2003 at Tooloom National Park (28°28'S, 152°25'E; altitude ~400 m) in northeastern New South Wales, Australia (Borgia, 1985b). The area consists largely of temperate rainforest and mesic eucalyptus woodland. Bowerbirds were caught with baited traps at feeding sites prior to the start of the mating season. Unmarked birds were fitted with a unique color band

combination (Borgia, 1985b) and a numbered aluminum band. We recorded mass, tarsus and wing length and several other morphological characters, and counted ectoparasites (Borgia, 1986; Borgia and Collis, 1989). Birds used in aerobic performance studies were held in cloth bags in a quiet, dark, cool location for up to 1 h before testing. All birds were released immediately after measurements were completed. Capture and handling procedures were approved by Australian wildlife authorities (University of Wollongong, New South Wales National Parks, Australian Bird and Bat Banding Scheme). All procedures complied with the Principles of Animal Care (publication no. 86-23, revised 1985) of the National Institutes of Health and were approved by the Institutional Animal Care and Use Committees of the University of Maryland and the University of California, Riverside.

Age and sex determination

We identified adult males from their blue-black plumage. Adult females were identified from plumage characteristics, bill and eye color, and behavior at bowers (females begin to breed in their second year). Young birds often cannot be sexed by plumage or morphology, although juvenile males older than ~4 years are usually identifiable (Vellenga, 1980). The sex of some birds captured as juveniles was subsequently determined from video records of behavior at bowers or from plumage at captures one or more years later. Bowerbird research began at the study site in the 1970s and the ages of many individuals were known from banding records. However, only a minimum age could be determined for birds initially captured as adults, such as those that migrated into the study area. Unmarked adult plumage males were at least 7 years old (Vellenga, 1980), but could be considerably older (several birds in the study area were more than 20 years old). For such individuals, we used the minimum known age.

Body condition and asymmetry

The ratio of mass to skeletal size is often used as an index of body condition (large mass in relation to skeletal size is usually assumed to indicate good condition). Similarly, morphological asymmetry is often assumed to indicate environmental stress or developmental instability (e.g. Van Valen, 1962; Møller and Swaddle, 1997). For satin bowerbirds we used the lengths of the left and right tarsus, measured with digital calipers, as an index of skeletal size. We also measured left and right wing lengths as a soft tissue size index (wing length largely consists of the length of primary feathers, which are re-grown during molting). Tarsus length was a better predictor of mass than wing length (Table 1), so we computed a body condition index as $\text{mass}/\text{mean tarsus length}^3$ (mass was measured in grams, tarsus length in centimeters). Tarsus asymmetry was computed as the percentage variation in left and right tarsus length as the absolute value of 100: $(\text{left tarsus length} - \text{right tarsus length})/\text{mean tarsus length}$, where no asymmetry = 0. We calculated wing length asymmetry in an identical manner.

Video monitoring

To determine which males owned bowers, and in some cases to determine sex (e.g. separating adult females from juveniles), we monitored all bowers in the study area (~30–35) throughout the mating season (early November until late December) using video cameras triggered by infrared sensors (Borgia, 1995).

Aerobic capacity

We measured aerobic capacity as maximum rate of oxygen consumption ($\dot{V}_{O_{2,\max}}$) using open circuit respirometry with an enclosed flight-running wheel serving as the metabolic chamber

Table 1. Correlations between \log_{10} body mass and two size indices, wing length and tarsus length, in wild-caught satin bowerbirds

	N	Tarsus length	N	Wing length
Adult males	48	0.193 ($P=0.044$)	45	0.115 ($P=0.79$)
Juvenile males	42	0.246 ($P=0.0012$)	41	0.036 ($P=0.34$)
Adult females	26	0.271 ($P=0.012$)	25	0.285 ($P=0.011$)
Juveniles (sex unknown)	226	0.404 ($P<0.0001$)	219	0.028 ($P=0.024$)
Pooled data	340	0.405 ($P<0.0001$)	330	0.118 ($P=0.029$)

Mean values [(left+right)/2] were used for wing and tarsus lengths. Models included measurement date, because mass declined over the study period (Fig. 1); the model for pooled data included age–sex class, as this also affects mass. Values shown are overall r^2 and significance of tarsus or wing length.

(Chappell et al., 1996; Chappell et al., 1999; Pierce et al., 2005; Wiersma et al., 2007). The wheel (inside diameter 52 cm, width 25.4 cm, volume 54 l, circumference 1.63 m) was constructed of PVC pipe with clear acrylic faceplates equipped with access doors. The perimeter was lined with thin carpet to provide traction and injury protection. Incurrent air entered through gas-tight axial bearings. Mixing of air was facilitated by diffusers on the input and output ports, plus the rotation of the wheel and movements of the bird. The wheel was rotated by the experimenter at speeds adjusted to match the behavior of the bird being tested.

Ambient air was supplied under positive pressure with a portable pump. Flow rate was adjusted to 14.61 min^{-1} with a needle valve, monitored with a Gilmont flow meter (Great Neck, New York, USA). Before and after field work, the flow meter was calibrated against a Tylan mass flow controller (Carson, CA, USA), at similar temperatures and atmospheric pressure as occurred during measurements (calibration did not shift during the study). Because of the high flow rate, remote location and limited access to desiccants, incurrent air was not dried. However, at the temperatures and humidities during the study, water vapor concentrations never exceeded 1.5% and were usually much less than 1% of air volume, so the error in measured flow rate induced by ambient water vapor content was small. Samples of $\sim 100 \text{ ml min}^{-1}$ of excurrent air were dried (Drierite; W. A. Hammond Drierite Co. Ltd, Xenia, OH, USA) and passed through the sensor of a Sable Systems oxygen analyzer (FC-1; Las Vegas, NV, USA). Output from the FC-1 was recorded every 1.0 s by a Macintosh laptop equipped with a National Instruments analog-to-digital converter and custom data acquisition software (<http://warthog.ucr.edu>). Several hundred readings were averaged for each recorded datum. With this signal averaging, the resolution of the system was better than 0.0015% O_2 .

The test procedure followed other studies that used flight wheels to measure $\dot{V}_{\text{O}_2, \text{max}}$ (Chappell et al., 1999; Hammond et al., 2000; Wiersma et al., 2007). Bowerbirds were weighed to $\pm 1 \text{ g}$ with a spring balance immediately before tests, then placed in the wheel (which was initially covered with cloth to reduce stress) and allowed several minutes to adjust while baseline O_2 concentration and ‘resting’ \dot{V}_{O_2} were measured. The wheel was then uncovered and rotated slowly until the bird oriented to the movement and walked or ran to maintain position. This generally required 15–30 s. Subsequently speed was gradually increased while \dot{V}_{O_2} and behavior were monitored; at all but the lowest speeds, most birds flapped (sometimes extensively) in addition to running. We assumed that $\dot{V}_{\text{O}_2, \text{max}}$ had been attained when \dot{V}_{O_2} did not increase with increasing speed, or when birds no longer maintained coordinated locomotion or position in the wheel. Birds showed obvious signs of exhaustion at this point (intense panting with gaped mouth, drooped wings or prone posture), but they recovered quickly. Complete measurements lasted 4–8 min (1.5–5 min of wheel motion). A few birds refused to exercise in the wheel and data from these individuals were not used.

We computed \dot{V}_{O_2} using LabAnalyst software (<http://warthog.ucr.edu>). Raw oxygen concentration data were baseline-corrected and smoothed to remove electrical noise. To improve system response time we did not remove CO_2 from sampled air and used the ‘Mode 2’ equation in LabAnalyst to convert O_2 concentration and flow rate into \dot{V}_{O_2} , assuming the respiratory quotient (RQ) was 0.85. For real RQ between 0.7 and 1.0, that assumption introduces a maximum potential error of 3% in \dot{V}_{O_2} calculations. Because birds were exercised in a consistent manner and exhibited qualitatively similar behavioral and metabolic responses, the error for among-bird comparisons was probably less than 1%. Wheel volume was large relative to flow rate, so to compensate for mixing and resolve short-term changes in \dot{V}_{O_2} , we calculated ‘instantaneous’ \dot{V}_{O_2} (Bartholomew et al., 1981). The effective volume of 56 liters was obtained from washout curves from near-instantaneous injections of oxygen-depleted air (Bartholomew et al., 1981). We computed $\dot{V}_{\text{O}_2, \text{max}}$ as the highest instantaneous \dot{V}_{O_2} averaged over continuous 1 min intervals (Chappell et al., 1995; Chappell et al., 1999; Wiersma et al., 2007).

Statistics

Untransformed data were used for comparisons of body mass. Because avian exercise metabolism is a power function of mass (Tucker, 1970; McKechnie and Swanson, 2010), we used \log_{10} values of mass and $\dot{V}_{\text{O}_2, \text{max}}$ in most analyses to linearize relationships (back-transformed results are shown in the tables). For all tests other than repeatability, we used a single datum point for each individual. For body mass, we used the mass at initial capture; for aerobic capacity we used the highest $\dot{V}_{\text{O}_2, \text{max}}$ measurement of each individual (if this was tested on several dates in repeatability studies) and the associated body mass, wing and tarsus length, parasite count, etc. (analyses including all data points yielded qualitatively similar results). For comparison between age and sex classes, we used ANOVA or ANCOVA as appropriate. Residuals of these analyses were used to test for repeatability of mass and $\dot{V}_{\text{O}_2, \text{max}}$. Similarly, residuals from ANCOVAs including age–sex class and measurement date were used to test for repeatability of the body condition index.

Parasite counts were not normally distributed (zero-inflated) and for most age–sex classes could not be normalized by transformations. These data were analyzed with the SAS GENMOD (SAS Institute, Cary, NC, USA) procedure using a zero inflated Poisson distribution. Results are reported as a combination of a zero-inflation component (i.e. parasitized *versus* no parasites) and a Poisson component (numbers of parasites).

Calculations were performed with JMP 8 or SAS software. The significance level was 0.05 and data are given as means \pm s.d., unless otherwise noted.

RESULTS

Over the three field seasons we obtained 479 measurements from 358 satin bowerbirds in four age–sex classes (52 adult males, 28

Table 2. Body mass (g) in wild-caught satin bowerbirds

	N	Mean \pm s.d.	Range	Adjusted mean \pm s.e.m.	Group
Adult males	52	220.4 \pm 14.5	192–251	219.4 \pm 1.4	A
Juvenile males	43	217.1 \pm 12.4	191–240	217.3 \pm 1.9	A
Adult females	28	208.3 \pm 12.9	180–242	205.5 \pm 2.3	B
Juveniles (sex unknown)	235	207.4 \pm 15.3	168–255	208.3 \pm 0.9	B

For individuals captured more than once, we used the body mass at initial capture. The adjusted mean is the least-squares mean from ANCOVA, with day of the year at capture as covariate. Age–sex classes with the same group letter do not differ significantly in mass ($P>0.3$); classes with different letters are significantly different ($P<0.0001$).

adult females, 43 juvenile males and 235 juveniles of unknown sex). In 2001 we tested all captured bowerbirds and attempted to recapture and re-test as many individuals as possible to assess within-year repeatability. In 2002 and 2003, we continued to test all birds captured for the first time, and re-tested all birds measured in previous years. Consequently, few individuals were tested more than once per season in 2002 or 2003.

A few birds escaped after $\dot{V}_{O_{2,max}}$ testing but before completion of morphological measurements or ectoparasite counts, so sample sizes for the latter variables are slightly smaller than for body mass and $\dot{V}_{O_{2,max}}$.

Body mass and condition

Body mass ranged from 168 to 255 g (Table 2); both the heaviest and lightest individuals were juveniles. There were no body mass differences among years ($P=0.16$) and no year \times age–sex class interactions ($P=0.74$). Accordingly, we deleted year as a factor in subsequent analyses. Within years, body mass declined over the period of measurement (Fig. 1). Slopes of mass *versus* capture date regressions did not differ significantly among age–sex classes (mass \times date interaction, $P=0.24$), so we used a common-slope ANCOVA

in subsequent analyses. Both capture date ($F_{1,471}=19.9$, $P<0.0001$) and age–sex class ($F_{3,471}=20.2$, $P<0.0001$) significantly affected body mass. Within years, mass declined by an average of 13.4 g between the earliest and latest capture dates (6th September to 10th November; Fig. 1). Adult and juvenile males were significantly heavier than adult females or unknown-sex juveniles, but there was no difference between adult and juvenile males ($P=0.35$) or between adult females and unknown-sex juveniles ($P=0.34$; Table 2).

Among all individuals whose minimum age was known, there was a marginally significant tendency for mass to decline with increasing age after accounting for age–sex class and within-year capture date ($F_{1,174}=3.52$, $P=0.062$). The same was true for adult birds ($N=126$, $t=-1.97$, $P=0.0507$). However, mass was not related to age in adult males ($P=0.17$).

We used ANCOVA residuals to test for repeatability in mass among birds captured more than once. There were no significant effects of age–sex class on mass repeatability. Body mass showed significant repeatability both within years ($N=54$, $r=0.74$, $P<0.0001$; elapsed time between measurements 17.4 \pm 5.4 days) and between years ($N=79$, $r=0.61$, $P<0.0001$, elapsed time 310–786 days; mean 430 \pm 145 days, median 370 days).

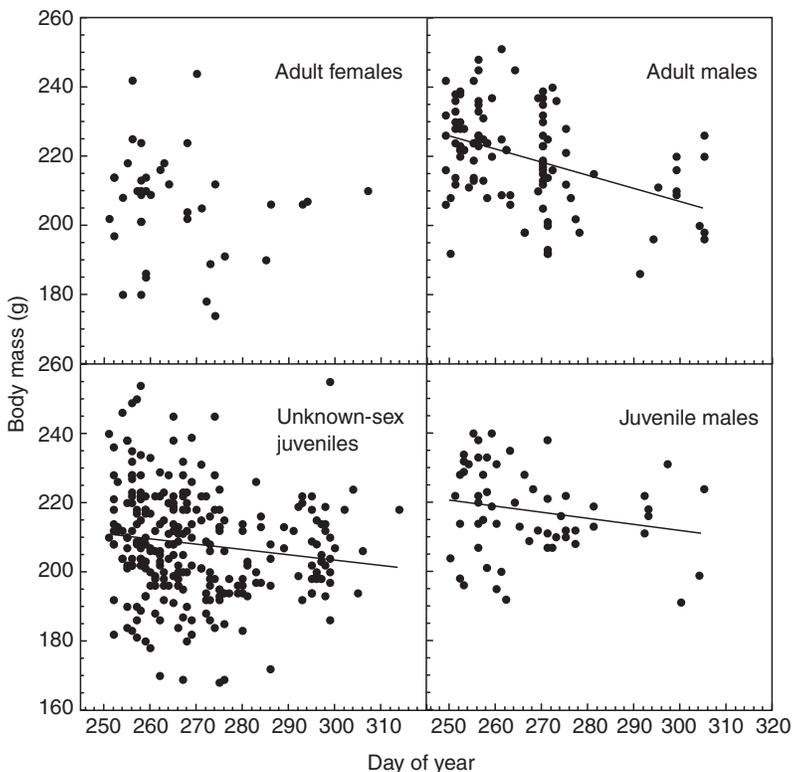


Fig. 1. Body mass of satin bowerbirds over the measurement period (September to November). All regressions except that for adult females are significant but slopes do not differ. Males (juvenile and adult) were significantly heavier than adult females and unknown-sex juveniles.

Table 3. Body condition index in wild-caught satin bowerbirds

	N	Mean \pm s.d.	Range	Adjusted mean \pm s.e.m.	Group
Adult males	48	1.64 \pm 0.03	1.25–2.17	1.62 \pm 0.03	A
Juvenile males	42	1.65 \pm 0.03	1.16–2.12	1.64 \pm 0.03	A
Adult females	26	1.91 \pm 0.04	1.43–2.45	1.88 \pm 0.04	B
Juveniles (sex unknown)	227	1.73 \pm 0.02	1.27–2.73	1.74 \pm 0.03	C

For individuals captured more than once, we used condition at initial capture. Condition was calculated as mass/(mean tarsus length)³ (g/cm³). The adjusted mean is the least-squares mean from ANCOVA, with day of the year at capture as covariate. Age–sex classes with the same group letter do not differ significantly ($P=0.61$); classes with different letters are significantly different ($P<0.007$).

Among the 343 individuals for which it was assessed, the body condition index was normally distributed, averaging 1.72 \pm 0.215 with substantial variation (range 1.15–2.73). It differed significantly among sex and age classes, with adult males having the lowest condition indices and adult females the highest ($F_{4,338}=12.4$, $P<0.0001$; Table 3). Within years in all age–sex classes, condition declined over time ($F_{4,338}=15.8$, $P<0.0001$), consistent with seasonal changes in body mass; there was no date \times age–sex class interaction ($P=0.30$). After accounting for age–sex class and within-year measurement date, the condition index was repeatable across years ($r=0.26$, $N=65$, $t=2.14$, $P=0.0363$). It was also significantly repeatable across years within adult females ($r=0.91$, $N=6$, $t=4.36$, $P=0.012$), approached significance in adult males ($r=0.32$, $N=32$, $t=1.85$, $P=0.074$), but was not repeatable in juvenile males ($N=13$, $P=0.84$) or juveniles of unknown sex ($N=14$, $P=0.61$).

Tarsus asymmetry was not affected by sex and age class and averaged 1.6%. There was no effect of year or sex and age class on tarsus asymmetry ($P>0.85$) and it was not repeatable for the pooled data or within an age–sex class ($P>0.35$). Wing length asymmetry was not affected by sex and age class ($P=0.29$), but there was a significant effect of year ($F_{2,299}=10.3$, $P<0.0001$). Wing length asymmetry was greatest in 2001 (1.06%) and considerably lower in 2002 and 2003 (0.46% and 0.22%, respectively). The overall mean was 0.85%, but a few birds with severe feather wear or damage had values of 6–14%. Wing length asymmetry was not repeatable for the pooled data set or within any age–sex class ($P>0.13$).

As previously reported (Borgia, 1986; Borgia et al., 2004), sex and age class significantly affected ectoparasite counts (Poisson component $\chi^2>70$, $P<0.0001$), with juvenile birds having higher counts than adults (mean 34.7, median 16, $N=268$ and mean 13.9, median 8, $N=77$, respectively). However, there was no effect of maturity on the presence or absence of parasites ($P=0.99$). Mass was not correlated with the presence or absence of parasites (zero-inflation $P=0.78$) but was negatively related to ectoparasite count after accounting for age–sex class (Poisson $\chi^2=5.77$, $P=0.016$). Ectoparasite count was negatively correlated with the condition index (zero-inflation $\chi^2=12.9$, $P=0.0003$; Poisson $\chi^2=576$, $P<0.0001$) and positively correlated with tarsus asymmetry (zero-inflation $P=0.27$, Poisson $\chi^2=19.4$, $P<0.0001$). Zero-inflation was minimal in the sample of birds caught in more than one year. Ectoparasite counts were repeatable across years in juveniles of unknown sex ($r=0.86$, $N=15$, $t=6.19$, $P<0.0001$) but not in adult males ($N=32$, $P=0.41$), adult females ($N=6$, $P=0.36$) or juvenile males ($N=12$, $P=0.37$).

Aerobic capacity

Preliminary tests showed no influence of capture date on $\dot{V}_{O_{2,max}}$ after accounting for the effects of body mass. A mixed-slope ANCOVA predicting $\dot{V}_{O_{2,max}}$ from body mass and age–sex class indicated that effects of mass on $\dot{V}_{O_{2,max}}$ did not differ significantly

among age–sex classes (mass \times class interaction $P=0.12$). Accordingly, we used a common-slope model in subsequent analyses. After accounting for mass and age–sex class, there was no significant effect of mean tarsus length ($P=0.80$), body condition index ($P=0.55$), tarsus asymmetry ($P=0.49$) or wing length asymmetry ($P=0.71$) on $\dot{V}_{O_{2,max}}$. Similarly, these variables had no effect when tested within any age–sex class and were deleted from subsequent analyses.

Body mass was significantly correlated to $\dot{V}_{O_{2,max}}$ (Fig. 2). The combined relationship for all 358 individuals was: $\dot{V}_{O_{2,max}}=0.62 \times \text{mass}^{0.791}$ (where $\dot{V}_{O_{2,max}}$ is in ml min⁻¹ and mass in g; $F_{1,356}=60.8$, $P<0.0001$; s.e. for exponent=0.102). For the 80 adult birds, the relationship was: $\dot{V}_{O_{2,max}}=0.91 \times \text{mass}^{0.729}$ ($F_{1,78}=13.6$, $P=0.0004$; s.e. for exponent=0.175). Age–sex class also affected $\dot{V}_{O_{2,max}}$ ($F_{4,353}=3.76$, $P=0.011$). There were no significant differences among adult females, juvenile males and unknown-sex juveniles, but adult males had 5–8% higher $\dot{V}_{O_{2,max}}$ than other classes (Table 3; Fig. 3; adult male $\dot{V}_{O_{2,max}}=0.59 \times \text{mass}^{0.814}$, $F_{1,50}=11.4$, $P=0.0014$; s.e. for exponent=0.241). Nevertheless, the two individuals with highest $\dot{V}_{O_{2,max}}$ were both juveniles (one male, one of unknown sex; Fig. 2). Although mass and age–sex class had significant effects and the overall model was highly significant ($F_{4,353}=18.4$, $P<0.0001$), it explained relatively little of the variance in $\dot{V}_{O_{2,max}}$ ($r^2=0.17$; Fig. 2).

After accounting for mass and age–sex class, the presence or absence of ectoparasites did not affect $\dot{V}_{O_{2,max}}$ (zero-inflation $P=0.26$), but there was a positive association between ectoparasite count and $\dot{V}_{O_{2,max}}$ across all age–sex classes (Poisson $\chi^2=22.8$, $P<0.0001$). Because female satin bowerbirds prefer males with low parasite loads (Borgia, 1986; Borgia and Collis, 1989) and aerobic performance conceivably could be a clue for identifying infection levels, we tested whether ectoparasite count affected $\dot{V}_{O_{2,max}}$ in adult males. It did not ($P=0.17$ after accounting for mass; in adult males a Box–Cox transformation normalized the ectoparasite count distribution and the relationship was tested with least-squares regression). Similarly, there was no effect of ectoparasite count on $\dot{V}_{O_{2,max}}$ in the 24 bower-holding males ($P=0.14$).

The birds' minimum age was known for 181 $\dot{V}_{O_{2,max}}$ measurements, so we tested for any influence of age with an ANCOVA including mass, age–sex class and age. There was no effect of age either for all 181 known-age birds ($t=0.47$, $P=0.49$) or for the 128 adults of known age ($t=-0.95$, $P=0.34$). A non-linear relationship between $\dot{V}_{O_{2,max}}$ and age could account for the absence of significant age effects in ANCOVA. However, plots of age versus mass-adjusted $\dot{V}_{O_{2,max}}$ revealed no indication of non-linear relationships within any age–sex class (e.g. adult males; Fig. 4).

To test for individual consistency of $\dot{V}_{O_{2,max}}$, we used residuals from an ANCOVA predicting $\dot{V}_{O_{2,max}}$ from mass and age–sex class for the entire dataset of 479 measurements. Repeatability of $\dot{V}_{O_{2,max}}$ was significant both within and between years (Fig. 5). For 54 individuals from all age–sex classes tested twice in the same year

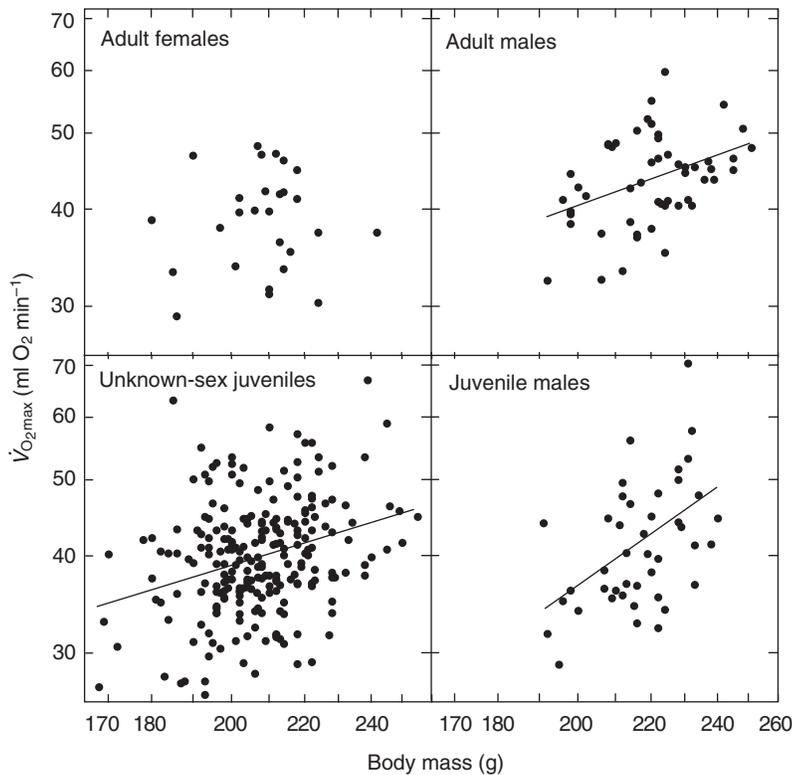


Fig. 2. Aerobic capacity measured as maximum rate of oxygen consumption ($\dot{V}_{O_{2,max}}$) in 358 satin bowerbirds of four age–sex classes. All regressions except that for adult females are significant but slopes do not differ.

(mainly in 2001), $r=0.648$, $t=6.19$, $P<0.0001$ (elapsed time between measurements 17.4 ± 5.4 days). For 52 individuals tested in at least two different years, $r=0.365$, $t=3.15$, $P=0.0023$ (79 comparisons; elapsed time 310–786 days, mean 430 ± 145 days, median 370 days). When analysis was restricted to adult birds only, repeatability remained significant both within ($N=36$, $r=0.71$, $t=5.84$, $P<0.0001$) and between years ($N=43$, $r=0.32$, $t=2.19$, $P=0.034$).

We explored possible explanations for the lower between-year repeatability compared with within-year repeatability by searching for relationships between inter-year changes in mass-adjusted $\dot{V}_{O_{2,max}}$ and changes in several indicators of condition (ectoparasite count, wing length asymmetry and the body condition index: mass/tarsus length³). We found no significant correlations between changes in any of these indices and changes in $\dot{V}_{O_{2,max}}$, although the effect of changes in the body condition index approached significance for all age–sex classes combined ($F_{6,58}=3.46$; $P=0.068$). Restricting the analysis to adult males revealed no significant predictors of changes in $\dot{V}_{O_{2,max}}$ ($P>0.39$ for all condition indices). Similarly, no significant predictors were found in other age–sex classes.

Bower ownership

Within the 52 adult males, there was no difference in $\dot{V}_{O_{2,max}}$ between bower-owning individuals ($N=24$) and non-owners ($P=0.56$ for $\dot{V}_{O_{2,max}}$ alone; $P=0.92$ with mass as covariate). Bower ownership was not correlated with ectoparasite loads, body mass, condition index, tarsus asymmetry or wing length asymmetry ($P=0.18$, $P=0.98$, $P=0.96$, $P=0.47$, $P=0.97$, respectively).

DISCUSSION

To our knowledge, this study of satin bowerbirds is the first report showing repeatability of avian aerobic capacity in a wild population, and is the largest sample of exercise $\dot{V}_{O_{2,max}}$ measurements in any bird species. We found differences between the aerobic performance

of adult males and that of all other sex and age classes, as well as significant repeatability over intervals of up to two years. Before discussing these results in detail, it is appropriate to comment on the $\dot{V}_{O_{2,max}}$ measurements themselves.

The value of any measurement depends on its reliability, and protocols that include a substantial behavioral component – such as our $\dot{V}_{O_{2,max}}$ tests – are susceptible to uncontrolled variability due to factors such as motivation. Our analyses assume that the measured $\dot{V}_{O_{2,max}}$ are accurate and sufficiently reliable for valid comparisons, both within our sample of satin bowerbirds and in relation to other studies. The latter issue is of particular importance because of the diversity of techniques used to elicit maximal exercise in birds. In addition to the ‘flight wheel’ approach, these include running on treadmills (e.g. Taylor et al., 1982; Brackenbury and El-Sayed, 1985), flight in wind tunnels (e.g. Tucker, 1970) and swimming in tanks or flumes (e.g. Kooyman and Ponganis, 1994). Usually such methods require intensive training and hence extended periods of captivity, which might induce conditioning artifacts. In contrast, flight wheels require no training and little time in captivity (only a few minutes) and therefore are particularly suitable for studies of free-living birds.

Forced exercise in a flight wheel may not be equivalent in power intensity to flapping flight, as important muscle groups are not used identically in the two behaviors. Nevertheless, several factors suggest that our protocol reliably elicited $\dot{V}_{O_{2,max}}$ in satin bowerbirds. First, flight wheels have been employed in several studies of avian $\dot{V}_{O_{2,max}}$ that encompassed species ranging in mass from 6.5 g to 1.2 kg (Chappell et al., 1996; Chappell et al., 1999; Pierce et al., 2005; Wiersma et al., 2007); these studies used the same techniques to elicit maximal exercise that we employed for bowerbirds. Second, our measured $\dot{V}_{O_{2,max}}$ are consistent with \dot{V}_{O_2} derived from treadmill and wind tunnel measurements of avian aerobic capacity (McKechnie and Swanson, 2010). Finally, although bowerbirds recovered quickly after the completion of exercise, they always showed clear behavioral

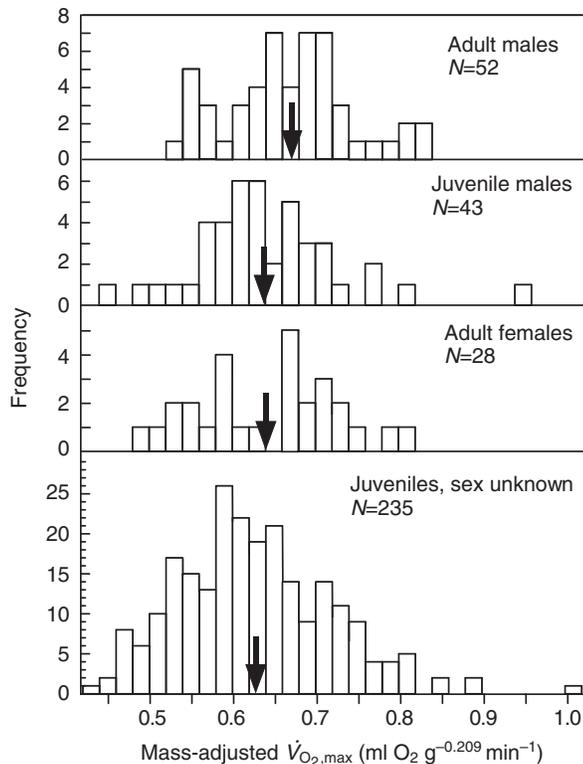


Fig. 3. Distribution of $\dot{V}_{O_2,max}$ for age and sex classes in satin bowerbirds. To compensate for mass differences among groups, $\dot{V}_{O_2,max}$ is shown scaled to the common mass exponent of 0.791. Mean values for each group are indicated by downward-pointing arrows. Adult males had significantly higher $\dot{V}_{O_2,max}$ than juvenile males, adult females and unknown-sex juveniles.

indications of exhaustion at the end of $\dot{V}_{O_2,max}$ tests (lack of response to wheel movement, loss of coordinated movement, intense panting, wing drooping and prone, sprawled posture). That indicates our protocol elicited a consistent physiological and behavioral end point, allowing valid comparisons among groups.

Aerobic capacity

Despite the rather small 1.5-fold range of body mass in our study, the $\dot{V}_{O_2,max}$ of satin bowerbirds scaled significantly to $mass^{0.791}$. That scaling coefficient is indistinguishable from the interspecific scaling to $mass^{0.804}$ for flight $\dot{V}_{O_2,max}$ and $mass^{0.783}$ for flight wheel $\dot{V}_{O_2,max}$ found by McKechnie and Swanson (McKechnie and Swanson, 2010). Despite the similarity, we caution that the correlation between $\dot{V}_{O_2,max}$ and body mass in satin bowerbirds, although significant, explained relatively little of the variance in $\dot{V}_{O_2,max}$, even after accounting for differences among sex and age classes (Figs 2, 3).

As mentioned above, several methods have been used to measure avian exercise metabolism, but most comparative analyses yield estimates of $\dot{V}_{O_2,max}$ close to what we found in satin bowerbirds. For the mean body mass of 212 g, recent allometries predict a $\dot{V}_{O_2,max}$ of $47.2 \text{ ml O}_2 \text{ min}^{-1}$ for trained birds tested during flight in wind tunnels and $35.6 \text{ ml O}_2 \text{ min}^{-1}$ in a flight wheel (McKechnie and Swanson, 2010); our value for freshly captured bowerbirds was $42.9 \text{ ml O}_2 \text{ min}^{-1}$. For adult male bowerbirds (mean mass 220 g), our value of $47.7 \text{ ml O}_2 \text{ min}^{-1}$ (Table 3) is close to the predicted $\dot{V}_{O_2,max}$ of $48.6 \text{ ml O}_2 \text{ min}^{-1}$ during flight and 30% higher than the prediction of $36.7 \text{ ml O}_2 \text{ min}^{-1}$ in flight wheels. From another perspective, the factorial aerobic scope for

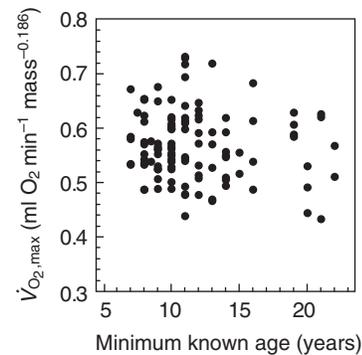


Fig. 4. Effect of age on mass-adjusted maximal aerobic capacity ($\dot{V}_{O_2,max}$) in adult male satin bowerbirds. Age is the minimum known age and was probably greater than shown here for some individuals, as males initially captured as adults (7 years or older) cannot be aged with certainty. Aerobic capacity was adjusted to the allometry for adult males ($\dot{V}_{O_2,max}$ scales with $mass^{0.814}$; see text). Although $\dot{V}_{O_2,max}$ tended to decline with age, the relationship was not significant ($P=0.17$).

exercise ($\dot{V}_{O_2,max}$ /basal metabolic rate; BMR) is 8–16 in most volant birds (Tucker, 1970; Brackenbury, 1984; Wiersma et al., 2007; McKechnie and Swanson, 2010). To our knowledge the BMR of satin bowerbirds has not been measured, so we used an allometrically derived BMR (McKechnie and Wolf, 2004). For adult males, predicted BMR was $3.02 \text{ ml O}_2 \text{ min}^{-1}$, giving an estimated aerobic scope of 15.8. For the other age–sex classes combined, mean body mass was 209 g, mean $\dot{V}_{O_2,max}$ was $43.1 \text{ ml O}_2 \text{ min}^{-1}$ and predicted BMR was 2.92, yielding a scope of 14.8.

Numerous studies have explored possible relationships of body condition, morphological asymmetry and parasite infestations with ecology, behavior or whole-organism physiology in a variety of taxa (e.g. Zuk et al., 1990; Gibson, 1990; Chastel et al., 1995; Chappell et al., 1996; Møller and Swaddle, 1997), including satin bowerbirds (Borgia, 1986; Borgia and Collis, 1989; Borgia et al., 2004). Our study population exhibited substantial variation in all these parameters, but we found no significant effects of condition or tarsus or wing length asymmetry on either aerobic performance (a highly integrative trait involving multiple organ systems) or bower ownership (an essential factor in male mating success). Unexpectedly, ectoparasite count was positively associated with aerobic performance, although there was no difference between parasitized and unparasitized birds. The overall effect was slight and was not significant in adult males. We were unable to show a significant relationship between ectoparasite infection and male $\dot{V}_{O_2,max}$; that finding does not support the possibility that females use male $\dot{V}_{O_2,max}$ to identify potential mates that are resistant to ectoparasite infection. Similarly, ectoparasite burdens were unrelated to whether an adult male was known to have a bower.

Repeatability of mass and condition

In order for a trait to respond to selection, it must be repeatable and heritable. Repeatability is a measure of the consistency of individual characteristics (such as performance or performance ranking within a population) over time and typically is considered to set the upper limit to heritability (Falconer and MacKay, 1996). That assumption may not always be valid (Dohm, 2002) and repeatable traits are not necessarily heritable. Nevertheless, repeatability provides an indication of the potential of a trait to respond to selection.

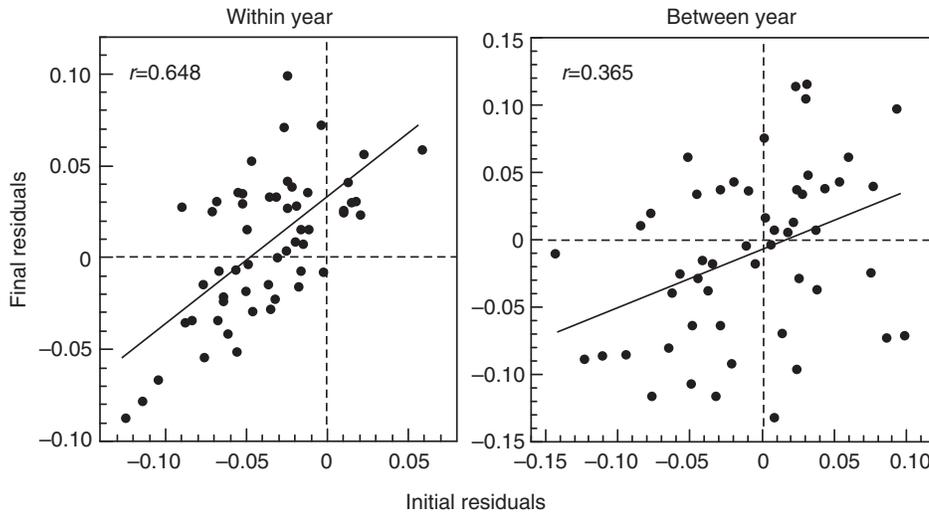


Fig. 5. Repeatability of aerobic performance ($\dot{V}_{O_2,max}$) within years ($N=55$, $P<0.0001$) and between years ($N=52$, $P=0.0078$). Residuals were generated from ANCOVA models incorporating sex and age class (adult male, adult female, juvenile) and body mass. ANCOVAs included all tested individuals (not just individuals with multiple measurements). Body mass and $\dot{V}_{O_2,max}$ were \log_{10} -transformed before analysis.

Although body mass is a fundamental organismal characteristic and impacts nearly all performance traits (especially metabolic rate), its repeatability is surprisingly little studied, particularly in wild populations. In captive mammals and birds, body mass is usually strongly repeatable over periods of days, weeks or months (Hayes and Chappell, 1990; Labocha et al., 2004; Hörak et al., 2002). Results from the relatively few field studies of mass repeatability are inconsistent. In bighorn sheep (*Ovis canadensis*) and male weasels (*Mustela nivalis*), body mass was highly repeatable in adults (Réale et al., 1999; Szafranska et al., 2007), but that of deer mice (*Peromyscus maniculatus*) was not repeatable (Hayes and O'Connor, 1999).

Analysis of mass repeatability in satin bowerbirds was complicated by size differences among age and sex classes, and by declines in mass across the September to November study period (Fig. 1). Nevertheless, after accounting for these factors, we found high repeatability both within and between years (elapsed times averaging 17 and >400 days, respectively). Between year repeatability ($r=0.61$) was only slightly less than within-year repeatability ($r=0.74$).

The body condition index (the ratio of mass to tarsus length) was repeatable across years in adult satin bowerbirds, but not juveniles. Thus adults tended to retain their condition over extended periods, but our data do not indicate if this was due to individual differences in genetically controlled traits or to environmental factors (e.g. possession of good *versus* poor territories or home ranges; variation in food supply or pathogen exposure when young). In either case, condition was not related to known bower ownership in adult males. Adult males had the lowest condition index scores among all age–sex classes (Table 3), which could be interpreted as indicative of high energy demands for inter-male competition. However, the condition score of adult males did not differ from that of juvenile males, which do not compete for matings or bowers, and within-season rates of mass loss of adult males did not differ from those of other age–sex classes (Fig. 1). A second condition index, wing length asymmetry, showed no repeatability in any age–sex class. Asymmetry of wing length probably results partially from uneven feather wear, but because molt occurs after the breeding season, it might also reflect stress in the previous mating season that affected feather growth.

Ectoparasite counts were repeatable across years in juveniles of unknown sex ($N=15$, $t=6.19$, $P<0.0001$) but not in adult males ($N=32$, $P=0.41$), adult females ($N=6$, $P=0.36$) or juvenile males ($N=12$, $P=0.37$). A ten-year study of the same population found no repeatability between the juvenile phase and adulthood (Borgia et al.,

2004). Lack of repeatability in adult males is of interest, since female satin bowerbirds have an apparent preference for males with low ectoparasite loads (Borgia, 1986; Borgia and Collis, 1989). Repeatability might be expected if females use the ectoparasite burden of a prospective mate as an indicator of his genetic ability to resist infection. Females may also favor males with low ectoparasite loads in order to reduce their own probability of infection (Borgia and Collis, 1989). The lack of repeatability in our data might reflect year-to-year variation in the abundance of parasites, and not inconsistency in infection resistance. Moreover, this population generally has low levels of infection in adult males, which makes it difficult to demonstrate repeatability (Borgia, 1986; Borgia and Collis, 1989; Borgia et al., 2004).

Repeatability of $\dot{V}_{O_2,max}$

Comparative physiologists have traditionally considered metabolic traits – especially those that seem specialized for particular environments or behaviors – as the results of adaptive evolution. Despite the importance of repeatability for responses to selection, rigorous testing of metabolic rate repeatability (and to a lesser extent, heritability) has become widespread only in the last two decades, with greater emphasis on laboratory-housed animals than on wild populations. In general, these studies have revealed substantial repeatability of the extremes of aerobic metabolism ($\dot{V}_{O_2,max}$ elicited by cold or exercise, and BMR or resting metabolic rate) (Hayes and Chappell, 1990; Chappell et al., 1995; Chappell et al., 1996; Bech et al., 1999; Hayes and O'Connor, 1999; Labocha et al., 2004; Rønning et al., 2005; Szafranska et al., 2007; Evans and Rose, 2010), although repeatability was not found in some species (Swanson and Weinacht, 1997; Russell and Chappell, 2007). In several species, including both laboratory and natural populations, BMR or $\dot{V}_{O_2,max}$ remained highly repeatable across much of the life span (Szafranska et al., 2007; Rønning et al., 2005). In others, repeatability declined over time (Chappell et al., 1995; Bech et al., 1999; Hörak et al., 2002; Vézina and Williams, 2005).

Repeatability of $\dot{V}_{O_2,max}$ in satin bowerbirds followed the latter trend: it was substantial within a breeding season and, although lower, remained significant between years (Fig. 5). Significant repeatability satisfies an important requirement for $\dot{V}_{O_2,max}$ to be affected by selection, but we caution that repeatability does not necessarily mean a trait is heritable: non-genetic factors (e.g. maternal effects, rearing conditions, etc.) may have long-lasting influences that confer repeatability.

The decline in repeatability over time is interesting, since it does not always occur in other species, and of potential significance for selection on $\dot{V}_{O_{2,max}}$. This might be considered in terms of two contrasting hypotheses. One posits that $\dot{V}_{O_{2,max}}$ is largely genetically determined (i.e. highly heritable), but with age-related changes due to modulation of gene expression that reduce repeatability over time. That hypothesis predicts a consistent – but possibly nonlinear – relationship between $\dot{V}_{O_{2,max}}$ and age. However, in the pooled dataset we did not find significant correlations between $\dot{V}_{O_{2,max}}$ and minimum known age across a span of 5–22 years, and there was no apparent pattern in the relationship between $\dot{V}_{O_{2,max}}$ and age within any age–sex class (e.g. Fig. 4). The second hypothesis is that $\dot{V}_{O_{2,max}}$ is strongly affected by environmental conditions or other ecological factors and hence has low heritability. This hypothesis would be supported if inter-year variation in body condition – which presumably is influenced by environmental factors – was correlated with changes in $\dot{V}_{O_{2,max}}$. We found no significant correlations between changes in $\dot{V}_{O_{2,max}}$ and changes in any of three body condition indices that could be affected by environmental conditions: ectoparasite loads, wing length asymmetry and the body condition index (mass/tarsus length³). There was a trend in the pooled data for a positive relationship between changes in $\dot{V}_{O_{2,max}}$ and changes in the body condition index ($P \sim 0.07$): birds with improved condition showed better performance. However, among adult males (the age–sex class with the largest number of inter-year repeat measurements), there was no association between changes in any condition index and changes in $\dot{V}_{O_{2,max}}$. Moreover, adult males had the highest $\dot{V}_{O_{2,max}}$ among all age–sex classes, but the lowest condition indices; again indicating that aerobic performance was not closely linked to condition (at least as we estimated it). Thus our data are not clearly consistent with either hypothesis. Given the multiple factors underlying a complex whole-organism trait such as aerobic capacity, it is probable that gene \times environment interactions are important in the reduction of $\dot{V}_{O_{2,max}}$ repeatability over time.

Several other aspects of satin bowerbird $\dot{V}_{O_{2,max}}$ repeatability are of interest. When analysis was restricted to adults (minimizing any effects of maturational events that might be expected in juveniles), repeatability remained significant, both within and between years. That implies that the transition to adulthood does not entail major shifts in performance rankings, even though average $\dot{V}_{O_{2,max}}$ increases slightly when males become mature (Fig. 3). Huey and Dunham, and Rønning et al. suggested that in order to be responsive to selection, a trait should be repeatable over a timescale within which selection can be expected to occur (Huey and Dunham, 1987; Rønning et al., 2005). Depending on species, this may be brief (e.g. within a mating season) or extensive (e.g. lifelong exposure to factors such as temperature or predation). We found $\dot{V}_{O_{2,max}}$ repeatability across one or more breeding seasons, which for adult satin bowerbirds – especially males – is probably the period most crucial for fitness. We assume that is sufficient for selection to ‘see’

individual differences in aerobic performance, especially if they affect important events such as territoriality, mating or rearing offspring. Nevertheless, it should be noted that although our between-measurement period of up to 2 years for satin bowerbirds is long in relation to the intervals encompassed by most repeatability studies [comparable to the longest period over which BMR repeatability has been tested (Rønning et al., 2005)], it is not a large fraction of life span (or even reproductive life span) in these long-lived birds. The minimum known age of adults in our population averaged 11.2 ± 4.0 years and the true mean age was undoubtedly somewhat older. Whether $\dot{V}_{O_{2,max}}$ is repeatable over the lifetime of a bowerbird, which can exceed 20 years, is an open question.

High aerobic capacity in adult males

In some respects, the 5–8% higher mass-adjusted $\dot{V}_{O_{2,max}}$ in adult males is surprising. Powered, flapping flight is thought to be the most energetically demanding form of sustained exercise in vertebrates, and sustained exercise of any kind is strongly dependent on ATP produced in aerobic metabolism. Hence, aerobic capacity in volant birds should largely be a function of flight propensity and ability. Once they have fledged, all age and sex classes of satin bowerbirds are strong fliers and routinely use flight to move around their home ranges; also, seasonal migrations occur in parts of the species’ distribution (Cooper and Forshaw, 1977) (G.B., personal observation). Because there does not seem to be any age or sex-related variation in flight ability, one would expect no differences in the physiological capacity to support aerobic exercise. Moreover, apart from coloration and slightly larger body size, adult males show no obvious divergence in external morphology from females or juveniles.

Given their similarity to other age and sex classes in overall morphology and apparent flight ability, what other factors might explain the significantly higher $\dot{V}_{O_{2,max}}$ in adult males? Our results do not provide a conclusive answer, but several possibilities can be considered. One is that elevated $\dot{V}_{O_{2,max}}$ has no direct significance for survival or mating success, and instead is an artifact some other aspect of the physiology or morphology of adult males. For example, if males have less metabolically inactive body fat than other age–sex classes, they would probably have higher $\dot{V}_{O_{2,max}}$ after adjusting for body mass. Low fat content should be reflected in low condition scores, and adult males do have the lowest condition index of any age–sex class (Table 3). However, condition scores were not consistent with $\dot{V}_{O_{2,max}}$ differences across other age–sex classes (juvenile males have low condition scores but also relatively low $\dot{V}_{O_{2,max}}$; Table 4). Possibly, high androgen levels or other endocrine factors in adult males could induce increased muscle mass or power density. There is little evidence of a relationship between testosterone and aerobic capacity in birds (e.g. Chappell et al., 1997; Buttemer et al., 2006), but, subjectively, male satin bowerbirds seem much stronger than females when held in the hand (G.B. and J.-F.S., personal observations).

Table 4. Maximum oxygen consumption ($\dot{V}_{O_{2,max}}$; mlO₂ min⁻¹) in wild-caught satin bowerbirds

	N	Mean \pm s.d.	Range	Adjusted mean \pm s.e.m.	Group
Adult males	52	47.7 \pm 5.9	37.1–59.6	45.9 \pm 0.9	A
Juvenile males	43	45.7 \pm 7.2	32.3–70.35	43.7 \pm 1.0	B
Adult females	28	43.9 \pm 5.6	33.5–55.1	43.8 \pm 1.2	B
Juveniles (sex unknown)	235	43.7 \pm 6.6	27.5–67.1	42.6 \pm 0.4	B

For individuals tested more than once, we used the highest value of $\dot{V}_{O_{2,max}}$ and the associated body mass. The adjusted mean is the least-squares mean from ANCOVA with body mass as covariate (the analysis used log₁₀ values of mass and $\dot{V}_{O_{2,max}}$; back-converted results are shown here). Age–sex classes with the same group letter do not differ significantly in mass ($P > 0.3$); classes with different letters are significantly different ($P < 0.011$).

Predators might also affect male aerobic capacity. The conspicuous coloration of adult males, as well as the vocalizations and other noises inherent in courtship displays, may increase their risk of predation. Thus males who have been courting intensely might have to immediately fly to escape predators attracted to the sounds of the display, and higher $\dot{V}_{O_{2,max}}$ may be advantageous. If males with relatively low $\dot{V}_{O_{2,max}}$ are at higher risk, disproportionate mortality of these low-performing individuals could account for the higher mean $\dot{V}_{O_{2,max}}$ of adult males even if aerobic performance is not heritable. Conversely, males flying to their bower may need to display immediately to a visiting female; in this context elevated $\dot{V}_{O_{2,max}}$ would also be beneficial.

Speculatively, high $\dot{V}_{O_{2,max}}$ might increase male competitive ability or could affect both sexes in female choice. Males compete both directly (e.g. fighting during territoriality or bower defense; chasing other males) and indirectly (e.g. finding or stealing bower decorations) (Borgia and Gore, 1986), and high male $\dot{V}_{O_{2,max}}$ occurs in another bird with intense inter-male competition (red junglefowl) (Chappell et al., 1996; Chappell et al., 1997). However, the lack of $\dot{V}_{O_{2,max}}$ differences between bower-owning males and those not known to be bower owners suggests that aerobic capacity is not a primary determinant of inter-male competitive success in satin bowerbirds. Conceivably, females might use $\dot{V}_{O_{2,max}}$ to judge male quality, because aerobic capacity depends on many organ systems and hence could be an honest signal of health and vigor. If females make mating decisions based on male $\dot{V}_{O_{2,max}}$, then they need an ability to assess it, perhaps by evaluating the intensity or other characteristics of displays. Testing that hypothesis requires detailed study of male displays and female responses, along with aerobic physiology (J.-F.S., unpublished data). Such an analysis is beyond the scope of this paper, but it is noteworthy that females of two bowerbird species prefer males that display at high intensity (Borgia, 1995; Patricelli et al., 2002), as is also the case for sage grouse (*Centrocercus urophasianus*), a lekking species with similarly low male parental investment (Gibson et al., 1991). However, our subjective impression is that male courtship displays, although vigorous, are not as intense or energetically demanding as flapping flight or exercise in our flight wheel (males never showed signs of exhaustion after courtship episodes, as they always did during wheel tests).

More broadly, whether and how the elevated aerobic capacity of adult male satin bowerbirds might have evolved depends on multiple factors. Heritability of $\dot{V}_{O_{2,max}}$ is necessary if it is to respond to selection, but another key issue – particularly for females if they use $\dot{V}_{O_{2,max}}$ to evaluate male quality during mate selection – is whether any associated costs of high $\dot{V}_{O_{2,max}}$ are substantial or minor. A common presumption in evolutionary biology is that increased performance requires tradeoffs (detrimental changes in other traits). One frequently proposed tradeoff for high $\dot{V}_{O_{2,max}}$ is a high ‘maintenance cost’ of the metabolic machinery underpinning aerobic power production. That cost would be manifested as elevated basal or resting metabolic rate, as in the ‘aerobic capacity’ model of endothermy (Bennett and Ruben, 1979). High resting or basal metabolism could reduce fitness if it resulted in increased food requirements or decreased fasting endurance. However, the evidence for a link between exercise, $\dot{V}_{O_{2,max}}$ and BMR in birds is both scarce and contradictory (Chappell et al., 1999; Hammond et al., 2000; Wiersma et al., 2007). Given the absence of a clear association between $\dot{V}_{O_{2,max}}$ and BMR, it seems unlikely that the ~5% higher $\dot{V}_{O_{2,max}}$ of male satin bowerbirds engenders a substantial maintenance cost.

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