

Sex-specific development of avian flight performance under experimentally altered rearing conditions

Jan J. Verspoor,^a Oliver P. Love,^a Eloise Rowland,^a Eunice H. Chin,^b and Tony D. Williams^a

^aDepartment of Biological Sciences, Simon Fraser University, Burnaby, 8888 University Drive, British Columbia V5A 1S6, Canada, and ^bZoology Department, University of British Columbia, British Columbia V6T 1Z4, Canada

Numerous studies have examined predation risk resulting from the costs of impaired flight performance associated with many key life-history stages such as reproduction and migration. Interestingly, although avian nestlings experience multiple resource-based physiological trade-offs and undergo considerable morphological and physiological changes during postnatal development, there is no data available on how nestlings manage the competing demands of growth and the development of flight ability at this critical life-history stage. We examined numerous morphological traits to determine which are responsible for variation in flight performance in juvenile European starlings (*Sturnus vulgaris*), a sexually size-dimorphic passerine. We then manipulated maternal quality during chick rearing (via feather clipping) to examine sex-specific sensitivity of fledgling flight performance to the quality of the rearing environment. Results suggest that the mechanics underlying variation in juvenile flight performance are relatively simple, being principally determined by the ratio of pectoral muscle mass to body mass (BM) and the surface area of the wings. Interestingly, although the maternal quality manipulation decreased BM and structural size in daughters, only the flight performance of sons was negatively affected. Our results suggest that a survival-related trait can be significantly affected in the larger sex when raised under stressful conditions. Furthermore, measuring only BM and structural size may not be sufficient in understanding how the sexes are affected by stressful rearing conditions in sexually size-dimorphic species. **Key words:** development, escape performance, European starling, flight ability, predation risk, sexual size dimorphism. [*Behav Ecol* 18:967–973 (2007)]

In birds, flight performance, specifically takeoff velocity and angle of trajectory, determines escape ability and predation risk (Lima and Dill 1990; Lima 1993; Witter et al. 1994; Walker et al. 2005). Takeoff is one of the most energetically demanding modes of flight (Dial and Biewener 1993), and thus, one should expect escape ability to be under strong selection during those life-history stages when multiple physiological functions compete for finite energy resources or when there are marked changes in body mass (BM) (e.g., during reproduction, migration, or/and molt). For example, gravid female birds support a greater BM without a compensatory increase in flight muscle mass, resulting in a higher wing loading and compromised flight performance (Lee et al. 1996; Kullberg, Houston, and Metcalfe 2002; Kullberg, Metcalfe, and Houston 2002; Kullberg et al. 2005). It has even been suggested that female birds may deplete protein from the pectoral muscles required for flight to meet the protein demands of egg laying (Houston et al. 1995; Veasey et al. 2000, 2001). Similarly, temporarily high fuel loads (fat mass) generated seasonally in migratory species results in decreased flight performance (Piersma and Lindstrom 1997; Lind et al. 1999; Kullberg et al. 2000; Burns and Ydenberg 2002). Molt represents another physiologically demanding stage of the avian annual cycle when changes in wing loading, via a change in wing area rather than a change in BM, could influence flight performance (Lind and Jakobsson 2001). However, although studies suggest that wing loading increases during natural molt, there

appears to be no associated effect on takeoff performance (Lind 2001; Williams and Swaddle 2003): compensation for the reduced wing area occurs through a reduction in BM and an increase in flight muscle mass (Lind and Jakobsson 2001).

Avian nestlings experience multiple resource-based physiological trade-offs (Saino et al. 1997; Fargallo et al. 2002; Soler et al. 2003) and undergo considerable morphological and physiological changes during postnatal development (Ricklefs 1968, 1979a, 1979b, 1998; Ricklefs and Wermiuk 1977; Ricklefs and Peters 1979). Despite this, there is no data available on how nestlings manage the competing demands of growth and the development of flight ability at this critical life-history stage. In passerines, the developmental transformation from an immobile hatchling to a flight-capable fledgling is particularly rapid (Ricklefs 1979a, 1979b); yet at fledging, juveniles of many passerine species are closer to reaching adult BM than they are to completing wing development (Ricklefs 1968, 1979a, 1979b; Ricklefs and Peters 1979; data presented here). Therefore, given that a fledgling's first flights often occur before reaching full physiological or morphological maturity and that postfledging predation-induced mortality can be high (Naef-Daenzer et al. 2001), one would expect considerable selection on flight performance at this life-history stage.

In the present study, we investigated which morphological traits influence variation in juvenile flight performance in European starlings (*Sturnus vulgaris*) and whether the growth and flight performance of the sexes are differentially affected by an experimental manipulation of maternal rearing capacity. European starlings are sexually size dimorphic (Cabe 1993) and exhibit sex-specific growth patterns within the nest (Love et al. 2005) resulting in larger and heavier males at fledging (Chin et al. 2005; Love et al. 2005). In addition,

Address correspondence to O.P. Love. E-mail: olovea@sfu.ca. E.H. Chin is now at the Biology Department, Trent University, Peterborough, Ontario K9J 7B8, Canada.

Received 5 July 2006; revised 3 March 2007; accepted 5 March 2007.

nestlings of both sexes fledge before full developmental maturity is obtained (98–100% of adult tarsus length, 88–91% of adult BM, and 80–82% of adult wing length—data presented here). Theory also posits that the larger sex may be more sensitive to stressful or resource-limiting conditions during development (Richter 1983; Weatherhead and Teather 1991; Anderson et al. 1993; Torres and Drummond 1997, 1999; Velando 2002; although see Råberg et al. 2005). These combined traits make starlings an excellent model to examine developmental trade-offs between growth and flight ability at the time of fledging. Our study had 2 main goals: 1) to determine which morphological traits influence flight performance in a passerine at fledging and 2) to determine whether experimentally decreasing maternal quality (via wing clipping) reveals sex-specific sensitivity in development of flight ability. We predicted that the muscle mass:BM ratio and wing loading would play a significant role in juvenile takeoff ability. Likewise, and based on the conventional theory that the larger sex is more sensitive to a reduction in the quality of environmental conditions (Weatherhead and Teather 1991; Anderson et al. 1993; Torres and Drummond 1997, 1999; Velando 2002; Kalmbach et al. 2005; although see Råberg et al. 2005), we predicted that male starlings (sons) would show trait-specific sensitivity to the experimental decrease of maternal quality and hence may exhibit a greater decrease in flight performance while maintaining body size, whereas daughters would show the opposite relationship.

MATERIALS AND METHODS

Field site

Research for this study was conducted from April to July, 2005, at the Davistead dairy farm in Langley, British Columbia, Canada (49°10'N, 122°50'W) under a Simon Fraser University Animal Care permit (657B-96), following guidelines of the Canadian Council on Animal Care. The site contains 250 nest-boxes mounted on posts along the perimeter of 3 pastures and on farm buildings and barns throughout the site. The site is used yearly by a wild colony of breeding European starlings which lay 5.9 ± 0.2 (mean \pm standard error [SE]) eggs per clutch, incubate for 10.3 ± 0.1 days, and fledge chicks 22 ± 0.9 days after hatching (Love et al. 2005). Nest-boxes were checked daily to determine clutch initiation, laying sequence, and clutch completion dates. At day 10 of incubation, all eggs were removed from nest-boxes and placed in an incubator for approximately 24 h until hatching; painted wooden eggs were substituted for the removed eggs. At hatching, a blood sample was taken for sex determination. Nestlings were then returned to their nest and the wooden eggs removed. Nestling identity and subsequent age were tracked from hatch using nontoxic food coloring and chick-specific feather clipping until 10 days of age, at which time all chicks were banded to allow for subsequent identification of individual nestlings. In all nestlings, growth measurements (BM, beak length, tarsus length, and wing length) were taken at hatch and at a mean brood age of 5, 10, 15, and 17 days. Flattened wing chord replaced wing length measurements starting at 10 days of age when primary feathers began to appear. A large sample of unmanipulated nests ($n = 49$) was combined with the unmanipulated nests outlined below for the purpose of examining morphological traits that lead to variation in juvenile flight performance.

Manipulation of maternal rearing quality

Females were caught on the eighth day of incubation. Half of these birds underwent a feather-clipping treatment chosen

simply to reduce maternal chick-rearing quality as has been shown previously (Winkler and Allen 1995; Hill 2003). The treatment consisted of clipping the following feathers: the ninth, sixth, and third primary feathers, the sixth and third secondary feathers, and the sixth and third rectrices (tail feathers) near the base of each feather. Control birds were simply captured, measured, and released. Nests were divided randomly into the 2 treatment groups (control: 17 birds; clipped: 16 birds), and females were matched for laying date. All females were measured (beak length, tarsus length, wing chord, and BM), banded with metal and color bands to indicate individual and treatment identity, and then released near their nest-boxes where they were free to resume normal activities. Females were recaptured at days 7–8 of chick rearing (control: 17 of 17; clipped: 15 of 16) to determine any post-treatment change in BM; the remaining bird was not recaptured and had abandoned its nest. In order to assess parental provisioning rates, 30-min behavioral observations of each nest-box were performed using spotting scopes when chicks were aged between 6 and 8 days (i.e., during the linear growth phase of postnatal development); provisioning rate was calculated as the number of feeds per chick per hour (Chin et al. 2005; Love et al. 2005).

Flight performance trials

On the morning of the brood mean 21st day of age, juvenile birds were collected from their nest-box and transported in cloth bags (total time not exceeding 60 min) until the flight performance trials were conducted. The flight performance chamber was a $2.5 \times 1 \times 1$ -m wooden frame with fine plastic netting at the top and left end, black plastic sheeting at the bottom, clear plexiglass at the front, and a white plastic back with a 10×10 -cm lined grid on it. Conscious of the important difference between alarmed and nonalarmed (also called routine or spontaneous) flight (Kullberg et al. 1996, Kullberg 1998, Veasey et al. 1998, Nudds and Bryant 2002), we initially modeled our experimental design on that of Kullberg, Houston, and Metcalfe (2002) and Kullberg, Metcalfe, and Houston (2002), where the bird was released at the bottom of the vertical chamber and vertical takeoff ability was measured during the simulated escape flight. We adapted this design to release the birds using a dark box with trigger-release spring-loaded doors to eliminate any subjectivity associated with releasing the birds by hand. The doors simultaneously snapped open and produced a loud startle stimulus intended to initiate escape flight, designed to allow us to measure vertical takeoff ability as in Kullberg, Houston, and Metcalfe (2002) and Kullberg, Metcalfe, and Houston (2002). Although this method was effective for adult birds, fledglings proved incapable of sustained vertical takeoff, as when released they would either attempt to take off and come crashing back down or remain cowering in the box. For this reason, we rotated our chamber from a vertical to a horizontal position. It was also apparent that although obviously scared, the birds were not always initiating flight in response to the startle stimulus. Although some would fly immediately, many would cower for a brief period and then attempt fly, and yet others would simply remain cowering in the box. As such, we removed the spring-loaded box and instead released the birds into the chamber via a short (~ 30 cm long) tube, 10 cm in diameter, and aligned at a 30-degree incline designed to simulate the first flight from the nest-box. As a result of these changes, on release more than 90% fledglings would scramble up the tube and immediately launch into flight down the chamber and straight into the mesh at the end as though it was unseen. On a few occasions, the fledglings would pause momentarily at the end of the tube before launching into flight. This

behavior was typical of birds that could not fly, indicative of an uncertainty as to whether they were prepared for their first flight. In conjunction with this method of release, we experimented with various acoustic and visual startle stimuli but found none to have any bearing on initiating fledgling flight.

Flight was videotaped using a Sony TRV720 Digital 8 Video camera (at 30 frames/s) placed 2 m back from the clear plexiglass front of the flight chamber. To prevent habituation to the process, all fledglings were subjected to just 2 flight trials, of which we used the best trial as our measure of escape performance. On completion of the flight performance trials, fledglings were held in cloth bags until structural measurements (beak length, tarsus length, tail feather length, and flattened wing chord) and BM (to 0.01 g) were collected. A digital photograph of the left wing, standardized in a bent wing position against a scaled board, was taken to calculate wing area (using the total pixel method in Adobe Photoshop 7.0, Adobe Systems Inc., San Jose, CA). This allowed for the calculation of wing loading as the ratio of an individual's body weight to wing area (Pennycuik 1972). Birds were then collected (University of British Columbia Animal Care Permit, #A04-0277), carcasses were immediately refrigerated, and soon after, both the pectoralis major and supracoracoideus muscles, which together comprise the principal flight musculature, were removed from the right side of the bird's body via dissection. Fresh muscle mass was recorded to 0.0001 g and the tissue stored at -20°C . Birds were visually sexed based on the presence of testes or an ovary, and keel length measurement was taken prior to the carcass being frozen. Muscles were subsequently freeze-dried (Virtis Freezemobile model 8ES) and fat-extracted in a Soxhlet apparatus using petroleum ether to determine lean dry pectoral muscle mass (LDPM). We then calculated a pectoral muscle/BM ratio, here on referred to as the muscle:BM ratio, as follows:

$$\text{muscle/BM ratio} = (2 \times \text{LDPM}) / (\text{BM} - (2 \times \text{LDPM})). \quad (1)$$

LDPM was subtracted from the BM prior to calculation of the muscle:BM ratio to avoid statistical errors associated with part-whole correlation (Christians 1999).

Video analysis

Flight trials were analyzed on a TV monitor (Sony KV-27510) in the laboratory. Vertical displacements (to the nearest 2.5 cm) and associated times (to the nearest quarter frame) were measured relative to the 10-cm grid at 0.5 m horizontal intervals, with the center of the head used as a reference. Flight time taken per interval was thus calculated as the number of frames $\times 1/30$ s/frame. As the 0-m mark was set 0.21 m forward from where the bird emerged, analysis began after approximately one wing beat and once the bird's feet had left the perch. These parameters allowed the calculation of an average mechanical energy per unit mass (E) for each interval according to the equation from Williams and Swaddle (2003),

$$E = 1/2(V_x^2 + V_z^2) + gz, \quad (2)$$

where V_x and V_z are the horizontal and vertical components of flight velocity, respectively, g is the acceleration due to gravity, and z is height (Williams and Swaddle 2003). Units are in joules/kilogram (J/kg). This measure was chosen due to its ability to describe both the height and velocity gain components of flight performance in a single value (Williams and Swaddle 2003). Therefore, the energy gain between the first interval (0–0.5 m) and the third interval (1–1.5 m) was determined and used for the purpose of our study as a measure of overall flight performance (referred to hereafter as “flight

performance”). In all cases, the best performance from the 2 trials was taken.

Sex determination

As described previously, identification of the primary sex organs via dissection allowed for the determination of gender. To confirm that gender was assigned correctly, approximately half of the individuals were also sexed from the blood sample taken at hatching, using molecular methods based on polymerase chain reaction (PCR) amplification (Love et al. 2005). Briefly, DNA was isolated from the blood samples using Insta-gene matrix (Bio-Rad Laboratories, Hercules, CA, Cat. No. 732-6030) following the manufacturer's protocol. PCR amplification was carried out in a total volume of 10 μl and run using the P2 (5'-TCTGCATCGCTAAATCCTTT) and CW (5'-AGAAA TCATTCCAGAAGTTCA) primers. The sex assigned via the 2 techniques was the same in 100% of cases ($n = 86$ birds).

Statistical data analysis

We used general linear mixed models (GLMMs) to 1) examine sexual size dimorphism in nestlings, 2) determine which morphological traits influence flight performance, and 3) examine the effects of experimental manipulation of maternal quality on flight performance in male and female fledglings. All models were fitted using the restricted maximum likelihood procedure in JMP 6.0 (SAS Inc., Cary, NC), with “maternal identity” specified as a random term to control for nonindependence due to the inclusion of siblings in the analysis. Using a repeated-measures approach, we first confirmed the presence of sexual size dimorphism in both BM and structural size in fledgling nestlings, including developmental changes in BM or tarsus length as repeated measures, nestling sex as a fixed factor, and maternal identity as a random factor. We then used GLMM methods to examine which morphological traits contribute to flight performance of juvenile starlings. Explanatory variables considered (based on those known to influence flight performance in adults) were muscle:BM ratio, wing loading (cm^2/g), keel length (mm), and nestling sex (male or female). Models initially contained all explanatory variables and all 2-way interaction terms between sex and the other variables. A final model was selected by progressively eliminating nonsignificant interaction terms ($P > 0.05$) and then nonsignificant main effects until only significant terms remained: muscle:BM ratio, wing loading, and sex. Finally, we used GLMM to analyze sex-specific effects of the maternal quality manipulation on the morphological traits influencing flight performance and flight performance itself. Sex-specific sensitivity of flight performance to the experimental manipulation of maternal chick-rearing ability was analyzed by including sex and maternal feather-clipping treatment as fixed factors together with muscle:BM ratio and wing area included as covariates; maternal identity was again included as a random factor to control for nonindependence due to the inclusion of siblings in the analysis. Post hoc comparisons for significant interaction terms were carried out using the adjusted Bonferroni post hoc procedure, with the P value corrected for the number of pairwise comparisons made depending on the type of analysis (Rice 1989).

RESULTS

Determinants of and intersexual differences in flight performance

European starling nestlings in our population exhibited significant sexual dimorphism in growth rates during the linear phase of development (analysis of variance [ANOVA]: $F_{1,64} = 4.01$,

Table 1

Morphological traits of fledgling European starlings in relation to maternal quality treatment of their mother (control or clipped feathers; see Methods)

Trait	Male nestlings		Female nestlings	
	Control	Clipped	Control	Clipped
BM (g)	78.81 ± 1.3	76.91 ± 1.1	74.42 ± 0.9	70.71 ± 0.9*
Tarsus (mm)	35.68 ± 0.5	34.77 ± 0.5	34.95 ± 0.3	33.69 ± 0.2*
Wing cord (mm)	93.67 ± 1.3	91.72 ± 1.2	92.09 ± 0.6	89.12 ± 0.7*
Keel (mm)	31.28 ± 0.1	30.68 ± 0.2*	30.21 ± 0.16	29.82 ± 0.2

Least squares mean ± SEM are given.

* Significant differences of $P < 0.05$ within sexes across treatments.

$P < 0.05$; males: 5.94 ± 0.12 g/day; females: 5.54 ± 0.15 g/day—mean ± standard error of the mean [SEM]). As a result, the sexes exhibited significant divergence during development in BM (repeated-measures analysis of covariance [ANCOVA]: $F_{1,36} = 4.94$, $P = 0.03$; Table 1), tarsus length (repeated-measures ANCOVA: $F_{1,36} = 4.16$, $P < 0.05$; Table 1), and keel length (ANCOVA: $F_{1,36} = 5.12$, $P < 0.03$; Table 1), but not for flattened wing cord (ANCOVA: $F_{1,39} = 2.49$, $P = 0.12$; Table 1). In adult birds, the sexes differed in all traits measured: BM (ANOVA: $F_{1,29} = 21.7$, $P < 0.0001$; males: 86.87 ± 1.02 g, females: 79.92 ± 1.09 g—mean ± SEM), tarsus length (ANOVA: $F_{1,29} = 18.19$, $P = 0.0002$; males: 35.52 ± 0.20 mm, females: 34.25 ± 0.22 mm—mean ± SEM), and flattened wing cord (ANOVA: $F_{1,29} = 16.7$, $P = 0.0009$; males: 127.43 ± 0.74 mm, females: 123.4 ± 0.79 mm—mean ± SEM).

Examining correlates of flight performance in nestlings raised by unmanipulated mothers revealed that only muscle mass:BM ratio and wing loading predicted any of the variation in fledgling flight performance (ANCOVA: $F_{1,79} = 22.49$, $P < 0.0001$ and $F_{1,79} = 6.21$, $P = 0.01$, respectively). Separating wing loading into its 2 representative components indicated that only wing area contributed significantly to variation in flight performance (ANCOVA: $F_{1,79} = 7.52$, $P < 0.01$; BM: $F_{1,79} = 1.23$, $P = 0.27$). The sexes did not differ in the 2 traits determined to affect flight performance (ANCOVA: muscle mass:BM ratio: $F_{1,38} = 0.24$, $P = 0.63$; wing area: $F_{1,39} = 2.31$, $P = 0.14$). Finally, we found no difference between the sexes in flight performance when controlling for both wing area and muscle mass:BM ratio in nestlings raised by unmanipulated mothers (ANCOVA: $F_{1,79} = 1.29$, $P = 0.26$).

Manipulation of maternal quality and effects on offspring flight performance

The maternal feather-clipping manipulation resulted in a significantly larger decrease in maternal BM by the midchick-rearing stage compared with control (unclipped) mothers (ANOVA: $F_{1,14} = 4.42$, $P < 0.05$; clipped: 8.68 ± 1.23 g, unclipped: 5.31 ± 1.21 g—mean ± SEM). Furthermore, maternal provisioning rates (number of feeds/nestling/hour) of clipped mothers were significantly lower than that of control mothers (ANOVA: $F_{1,14} = 4.56$, $P < 0.05$). The maternal feather-clipping treatment affected male and female nestling structural size and flight performance differently. Although BM, tarsus, and wing cord of male fledglings were unaffected by the maternal treatment, female fledglings raised by wing-clipped mothers showed a significant reduction in all 3 traits compared with daughters raised by control mothers—BM (ANCOVA, maternal treatment × sex: $F_{1,72} = 4.21$, $P < 0.05$; Bonferroni post hoc analysis—male: $P = 0.6$, female: $P = 0.01$; Table 1), tarsus (ANOVA, maternal treatment ×

sex: $F_{1,72} = 5.34$, $P = 0.02$; Bonferroni post hoc analysis—male: $P = 0.45$, female: $P = 0.02$; Table 1), and wing cord (ANCOVA, maternal treatment × sex: $F_{1,72} = 4.89$, $P = 0.03$; Bonferroni post hoc analysis—male: $P = 0.5$, female: $P = 0.02$; Table 1). Interestingly, keel length was significantly smaller in males but not females (ANCOVA, maternal treatment × sex: $F_{1,75} = 7.16$, $P < 0.01$; Bonferroni post hoc analysis—male: $P = 0.02$, female: $P = 0.48$; Table 1). Despite the presence of sex differences in wing cord length, we did not detect any sex-specific treatment effects on either wing area (ANCOVA, maternal treatment × sex: $F_{1,75} = 3.21$, $P = 0.08$; Table 1) or muscle mass:BM ratio (ANCOVA, maternal treatment × sex: $F_{1,75} = 1.24$, $P = 0.27$; Table 1). However, as a result of lowered BMs yet similar wing areas, daughters raised by feather-clipped mothers had lower wing loading than daughters raised by control mothers, whereas sons showed no such difference across treatments (ANCOVA: maternal treatment × sex $F_{1,75} = 5.29$, $P = 0.02$; Bonferroni post hoc analysis—male: $P = 0.3$, female: $P = 0.016$). Finally, daughters showed no effects of the maternal feather-clipping treatment on flight performance, whereas flight performance of sons raised by feather-clipped mothers was significantly lower than fledglings raised by unmanipulated mothers (ANCOVA, maternal treatment × sex interaction: $F_{1,75} = 4.22$, $P < 0.05$; Bonferroni post hoc analysis—male: $P = 0.012$, female: $P = 0.4$; Figure 1A for males, Figure 1B for females).

DISCUSSION

To our knowledge, this study represents the first examination of the morphological correlates of flight performance in fledgling birds as well as the first investigation of potential sex-specific differences in juvenile flight performance in a sexually size-dimorphic species. Our results reveal that although the mechanics of flight appear to be similar to those observed in adult birds (Burns and Ydenberg 2002; Kullberg, Houston, and Metcalfe 2002; Kullberg, Metcalfe, and Houston 2002; Williams and Swaddle 2003; Kullberg et al. 2005), male and female juvenile starlings are faced with different challenges to their flight performance when faced with poor rearing conditions.

Morphological determinants of juvenile takeoff performance

Our results suggest that the mechanics underlying variation in fledgling flight performance are relatively simple, being principally determined by 2 morphological traits, muscle mass:BM ratio and wing area. Although studies on adult birds have measured numerous possible morphological traits that should influence variation in flight performance such as wing loading,

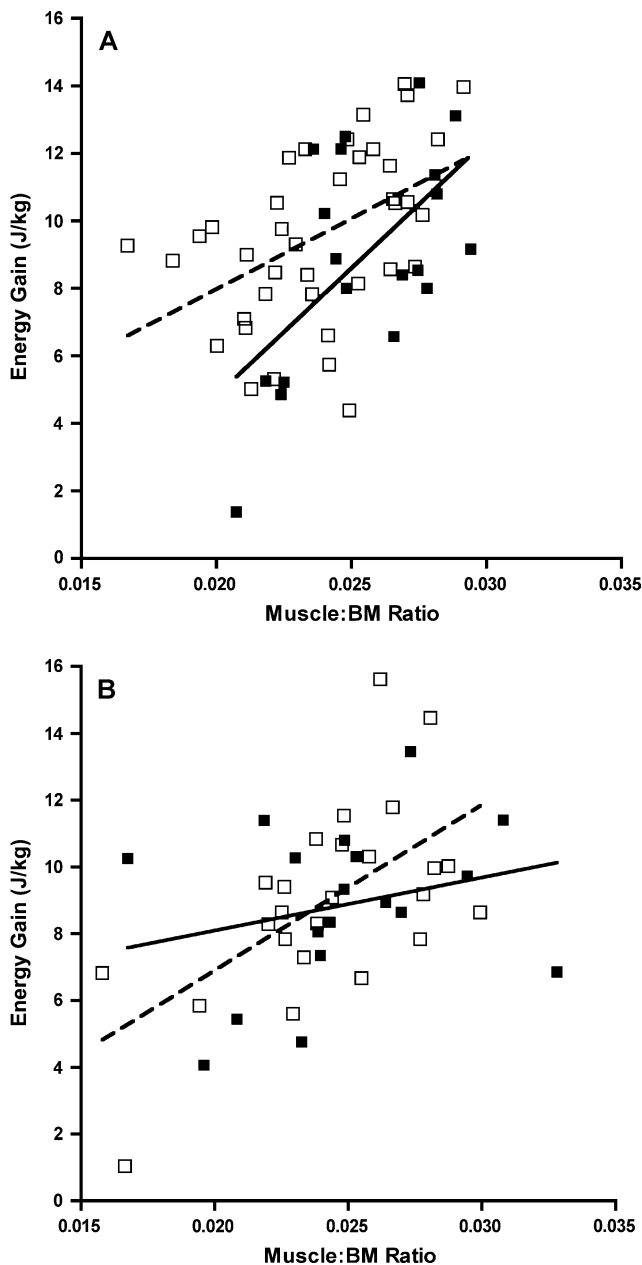


Figure 1
Sex-specific treatment effects of maternal feather clipping on (A) male and (B) female fledgling flight performance controlling for muscle:BM ratio. Solid squares and solid line represent fledglings raised by feather-clipped mothers, and open squares and dashed line represent fledglings raised by control mothers.

wing area, BM, muscle mass, and muscle mass:BM ratio (Lee et al. 1996; Lind et al. 1999; Swaddle et al. 1999; Kullberg et al. 2000, 2005; Lind and Jakobsson 2001; Veasey et al. 2001; Burns and Ydenberg 2002; Kullberg, Houston, and Metcalfe 2002), rarely do studies measure all potential determinants and attempt to separate the relative importance of each while controlling for the other determinants as we have done here. Furthermore, many studies ignore the role of pectoral muscle mass (e.g., Lee et al. 1996; Lind et al. 1999; Kullberg et al. 2000; Burns and Ydenberg 2002) or at best have attempted to estimate it from indirect measures (e.g., Veasey et al. 2001; Kullberg, Houston, and Metcalfe 2002; Kullberg, Metcalfe, and Houston 2002). Our analysis of intraspecific variation in

a juvenile passerine supports results by Marden (1987) which indicated that the flight muscle mass to BM ratio may be the single best determinant of interspecific variation in flight performance in adult birds. These results indicate that costs to flight performance have the potential to be detected at those life-history stages when the quality of the flight muscles can be significantly compromised (e.g., nestling growth, maternal fasting during incubation and migration). Practically speaking, our results further suggest that researchers should measure this ratio directly or at the very least use a meaningful indirect method.

Sensitivity of juvenile flight performance to reduced maternal quality

As previously reported, we found that male starlings exhibited faster growth rates during postnatal development (Love et al. 2005) and reached a larger BM and structural size by fledging compared with juvenile females (Chin et al. 2005; Love et al. 2005). Under stressful rearing conditions (maternal feather-clipping treatment), we found that male nestlings showed complete insensitivity in traits such as BM and structural size measures in response to decreased maternal quality. The structurally smaller female nestlings showed both reduced BM and structural size (tarsus, wing length) in relation to the experimental reduction in maternal quality. However, female nestlings raised by feather-clipped mothers showed no changes in wing area and no changes in muscle mass:BM ratio and exhibited no decreases in flight performance in relation to control female fledglings. However, male fledglings raised by feather-clipped mothers showed a significant decrease in flight performance compared with their control-raised counterparts. Our data are similar to the results recently reported by Chin et al. (2005) where large brood size in starlings did not affect male nestling body size but did result in compromised cell-mediated immune responses. These results suggest either 1) that the larger body size and mass in males important in mate competition (Cabe 1993; Love et al. 2005) has selected males to trade-off other morphological or physiological systems to maximize adult size (Chin et al. 2005; Love et al. 2005) or 2) that maximal flight is simply harder to perform in larger males that are raised under poor conditions.

Understanding the mechanism behind the reduction in male flight performance in response to decreased maternal quality is not entirely easy because males showed no decreases in wing area, wing loading, or muscle:BM. In fact, it was female fledglings raised by feather-clipped mothers that had lower wing loading as a result of decreased BMs and from first principles this result would suggest that daughters raised by low-quality mothers would actually show an increase in flight performance. The fact that we detected no differences in daughter performance yet a decrease in son flight performance suggests that the maternal treatment resulted in a decrease in the underlying mechanical structure or physiological functioning of the flight machinery that we were not able to measure. We suggest 2 possible preliminary explanations for our results. First, given that the maximal power output that a bird can generate for flight is dependent on both the flight muscles and the skeletal elements involved (Pennycuik 1972), it is possible that there was a sex-specific effect on physiological or mechanical performance in the muscle tissue itself, associated with the manipulation of maternal quality. It is well known that different muscle types can differ in traits such as fiber composition, myofibrillar stress capacity, fuel storage capacity, ability to accommodate an oxygen debt, or even tolerance of a temperature change (e.g., Pennycuik 1972; Swaddle and Biewener 2000; Williamson et al. 2001; Guglielmo et al. 2002). In particular, the fiber composition

of the flight musculature is highly variable between bird species (Norberg 1990). Although starling pectoral muscle consists exclusively of fast-twitch aerobic fibers (Norberg 1990; Swaddle and Biewener 2000), the muscle tissue can differ in both mitochondrial density and/or oxidative capacity, leading to variation in muscle performance (Swaddle and Biewener 2000). As such, a reduction in maternal quality may have affected physiological muscle performance in males more than females. We are presently conducting enzyme analyses of pectoral muscle samples to investigate this possibility. A second and mechanically simpler explanation may be that for a given muscle mass:BM ratio, the larger the length of the keel (sternum) bone, the greater the potential performance from the flight musculature. The sternum provides a large surface area for the origins of the pectoral muscles (Pennycuik 1972), and sternum size has been related with flight ability (Norberg 1990). Keel length was smaller in males raised by feather-clipped mothers, whereas female keel length was unaffected by the treatment. It is therefore possible that males raised under stressful conditions have a simple size-borne mechanical disadvantage over males raised under good conditions in that attaching the similar-sized pectoral muscle over a smaller keel length potentially results in a reduction in flight performance (Pennycuik 1972; Norberg 1990). Although this alternative hypothesis may seem less likely, it warrants further testing under field and possibly laboratory conditions to rule out.

The escape ability of many prey species is inextricably linked to their probability of survival when under attack from a predator (Lima and Dill 1990; Lind 2004; Walker et al. 2005) and flight performance can determine predation risk in birds (Rudebeck 1950; Witter et al. 1994; Lind 2004). Regardless of the mechanical or physiological mechanism discussed above, it appears that the larger sex nestlings in sexually size-dimorphic avian species face more potential costs in balancing growth and flight performance than the smaller sex. Future research should not only attempt to elucidate the basis of these costs but also examine how potential short-term performance deficits affect fledgling survival and even future performance as adults.

FUNDING

Natural Sciences and Engineering Research Council of Canada (NSERC) (31-611239 to T.D.W.), a graduate NSERC award (to E.C.), and a summer undergraduate NSERC award (to J.V.).

We are grateful to the Davis family at Davistead Dairy Farms, Langley, British Columbia, for their generous support of our starling field research. We would also like to thank L. Sheldon, K. Salvante, C. Stables, and E. Wagner for help with fieldwork; C. Semeniuk for the use of her video equipment; and D. Green for statistical and conceptual help with the manuscript. Finally, we would like to thank I. Owens, J. Lind, and an anonymous reviewer for help in improving the manuscript.

REFERENCES

- Anderson DJ, Reeve J, Gomez JEM, Weathers WW, Hutson S, Cunningham HV, Bird DM. 1993. Sexual size dimorphism and food requirements of nestling birds. *Can J Zool*. 71:2541–2545.
- Burns JG, Ydenberg RC. 2002. The effects of wing loading and gender on the escape flights of least sandpipers (*Calidris minutilla*) and western sandpipers (*Calidris mauri*). *Behav Ecol Sociobiol*. 52:128–136.
- Cabe PR. 1993. European Starling (*Sturnus vulgaris*). In: Poole A, Grill F, editors. *The birds of North America*. Philadelphia (PA): The Academy of Natural Sciences. p. 1–24.
- Chin EH, Love OP, Clark AM, Williams TD. 2005. Brood size and environmental conditions sex-specifically affect nestling immune response in the European starling (*Sturnus vulgaris*). *J Avian Biol*. 36:549–554.
- Christians JK. 1999. Controlling for body mass effects: is part-whole correlation important? *Physiol Biochem Zool*. 72:250–253.
- Dial KP, Biewener AA. 1993. Pectoralis muscle force and power output during the different modes of flight in pigeons (*Columba livia*). *J Exp Biol*. 176:31–54.
- Fargallo JA, Laaksonen T, Pöyri V, Korpimäki E. 2002. Inter-sexual differences in the immune response of Eurasian kestrel nestlings under food shortage. *Ecol Lett*. 5:95–101.
- Guglielmo CG, Haunerland NH, Hochachka PW, Williams TD. 2002. Seasonal dynamics of flight muscle fatty acid binding protein and catabolic enzymes in a migratory shorebird. *Am J Physiol*. 282:1405–1413.
- Hill H. 2003. Adjustments in parental care by the European starling (*Sturnus vulgaris*): the effect of female condition. *Proceedings of National Conference on Undergraduate Research (NCUR)*; 2003 March 13–15; Salt lake City, Utah (UT): University of Utah.
- Houston DC, Donnan D, Jones PJ. 1995. The source of the nutrients required for egg production in zebra finches *Poephila guttata*. *J Zool (Lond)*. 235:469–483.
- Kalmbach E, Furness RW, Griffiths R. 2005. Sex-biased environmental sensitivity: natural and experimental evidence from a bird species with larger females. *Behav Ecol*. 16:442–449.
- Kullberg C. 1998. Does diurnal variation in body mass affect take-off ability in wintering willow tits? *Anim Behav*. 56:227–233.
- Kullberg C, Fransson T, Jakobsson S. 1996. Impaired predator evasion in fat blackcaps (*Sylvia atricapilla*). *Proc R Soc Lond B*. 263:1671–1675.
- Kullberg C, Houston DC, Metcalfe NB. 2002. Impaired flight ability—a cost of reproduction in female blue tits. *Behav Ecol*. 13:575–579.
- Kullberg C, Jakobsson S, Fransson T. 2000. High migratory fuel loads impair predator evasion in sedge warblers. *Auk*. 117:1034–1038.
- Kullberg C, Jakobsson S, Kaby U, Lind J. 2005. Impaired flight ability prior to egg-laying: a cost of being a capital breeder. *Funct Ecol*. 19:98–101.
- Kullberg C, Metcalfe NB, Houston DC. 2002. Impaired flight ability during incubation in the pied flycatcher. *J Avian Biol*. 33:179–183.
- Lee SJ, Witter MS, Cuthill IC, Goldsmith AR. 1996. Reduction in escape performance as a cost of reproduction in gravid starlings, *Sturnus vulgaris*. *Proc R Soc Lond B Biol Sci*. 263:619–624.
- Lima SL. 1993. Ecological and evolutionary perspectives on escape from predatory attacks: a survey of North American birds. *Wilson Bull*. 105:1–47.
- Lima SL, Dill LM. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. *Can J Zool*. 68:619–640.
- Lind J. 2001. Escape flight in moulting Tree Sparrows (*Passer montanus*). *Funct Ecol*. 15:29–35.
- Lind J. 2004. What determines probability of surviving predator attacks in bird migration? The relative importance of vigilance and fuel load. *J Theor Biol*. 231:223–227.
- Lind J, Fransson T, Jakobsson S, Kullberg C. 1999. Reduced take-off ability in robins (*Erithacus rubecula*) due to migratory fuel load. *Behav Ecol Sociobiol*. 46:65–70.
- Lind J, Jakobsson S. 2001. Body building and concurrent mass loss: flight adaptations in tree sparrows. *Proc R Soc Lond B Biol Sci*. 268:1915–1919.
- Love OP, Chin EH, Wynne-Edwards KE, Williams TD. 2005. Stress hormones: a link between maternal condition and sex-biased reproductive investment. *Am Nat*. 166:751–766.
- Marden JH. 1987. Maximum lift production during take-off in flying animals. *J Exp Biol*. 130:235–258.
- Naef-Daenzer B, Widmer F, Nuber M. 2001. Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *J Anim Ecol*. 70:730–738.
- Norberg UM. 1990. *Vertebrate flight: mechanics, physiology, morphology, ecology and evolution*. Berlin (Germany): Springer-Verlag Press.
- Nudds RL, Bryant DM. 2002. Consequences of load carrying by birds during short flights are found to be behavioral and not energetic. *Am J Physiol*. 283:R249–R256.
- Pennycuik CJ. 1972. *Animal flight*. The institute of Biology's studies in Biology no. 33. London: Edward Arnold Ltd.
- Piersma T, Lindstrom A. 1997. Rapid reversible changes in organ size as a component of adaptive behavior. *Trends Ecol Evol*. 12:134–138.
- Räberg L, Stjernman M, Nilsson J-A. 2005. Sex and environmental sensitivity in blue tit nestlings. *Behav Ecol*. 14:496–503.
- Rice WR. 1989. Analyzing tables of statistical tests. *Evolution Int J Org Evolution*. 43:223–225.

- Richter W. 1983. Balanced sex ratios in dimorphic altricial birds: the contribution of sex-specific growth dynamics. *Am Nat.* 121: 158–171.
- Ricklefs RE. 1968. Patterns of growth in birds. *Ibis*. 110:419–451.
- Ricklefs RE. 1979a. Adaptation, constraint, and compromise in avian postnatal development. *Biol Rev Camb Philos Soc.* 54:269–290.
- Ricklefs RE. 1979b. Patterns of growth in birds. V. A comparative study of development in the starling, common tern, and Japanese quail. *Auk*. 96:10–30.
- Ricklefs RE. 1998. Avian growth and development: evolution within the altricial-precocial spectrum. New York: Oxford University Press.
- Ricklefs RE, Peters S. 1979. Intraspecific variation in the growth rate of nestling European Starlings. *Bird-Banding*. 50:338–348.
- Ricklefs RE, Weremiuk S. 1977. Dynamics of muscle growth in the starling and Japanese quail: a preliminary study. *Comp Biochem Physiol A*. 56:419–423.
- Rudebeck G. 1950. The choice of prey and modes of hunting of predatory birds with special references to their selective effect. *Oikos*. 2:65–88.
- Saino N, Calza S, Møller AP. 1997. Immunocompetence of nestling barn swallows in relation to brood size and parental effort. *J Anim Ecol.* 66:827–836.
- Soler JJ, de Neve L, Pérez-Contreras T, Soler M, Sorci G. 2003. Trade-off between immunocompetence and growth in magpies: an experimental study. *Proc R Soc Lond B Biol Sci.* 270:241–248.
- Swaddle JP, Biewener AA. 2000. Exercise and reduced muscle mass in starlings. *Nature*. 406:585–586.
- Swaddle JP, Williams EV, Rayner JMV. 1999. The effect of simulated flight feather moult on escape take-off performance in starlings. *J Avian Biol.* 30:351–358.
- Torres R, Drummond H. 1997. Female-biased mortality in nestlings of a bird with size dimorphism. *J Anim Ecol.* 66:859–865.
- Torres R, Drummond H. 1999. Does large size make daughters of the blue-footed booby more expensive than sons? *J Anim Ecol.* 72: 1133–1141.
- Veasey JS, Houston DC, Metcalfe NB. 2000. Flight muscle atrophy and predation risk in breeding birds. *Funct Ecol.* 56:883–889.
- Veasey JS, Houston DC, Metcalfe NB. 2001. A hidden cost of reproduction: the trade-off between clutch size and escape take-off speed in female zebra finches. *J Anim Ecol.* 70:20–24.
- Veasey JS, Metcalfe NB, Houston DC. 1998. A reassessment of the effect of body mass upon flight speed and predation risk in birds. *Anim Behav.* 56:883–889.
- Velando A. 2002. Experimental manipulation of maternal effort produced differential effects in sons and daughters: implications for adaptive sex ratios in the blue-footed booby. *Behav Ecol.* 13: 443–449.
- Walker JA, Ghalambor CK, Griscti OL, McKenney D, Reznick DN. 2005. Do faster starts increase the probability of evading predators? *Funct Ecol.* 19:808–815.
- Weatherhead PJ, Teather KL. 1991. Are skewed fledgling sex ratios in sexually dimorphic birds adaptive? *Am Nat.* 138:1159–1172.
- Witter MS, Cuthill IC, Bonser RHC. 1994. Experimental investigations of mass-dependent predation risk in the European starling, *Sturnus vulgaris*. *Anim Behav.* 45:201–222.
- Williams EV, Swaddle JP. 2003. Molt, flight performance and wing-beat kinematics during take-off in European starlings (*Sturnus vulgaris*). *J Avian Biol.* 34:371–378.
- Williamson MR, Dial KP, Biewener AA. 2001. Pectoralis muscle performance during ascending and slow level flight in mallards (*Anas platyrhynchos*). *J Exp Biol.* 204:495–507.
- Winkler DW, Allen PE. 1995. Effects of handicapping on female condition and reproduction in tree swallows (*Tachycineta bicolor*). *Auk*. 112:737–747.