Effects of simulated primary moult on pigeon flight

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Quantifying the costs and benefits of flight feather replacement is vital to our understanding of avian moulting patterns and life histories. This study investigated the effects of simulated primary moult on the flight ability of pigeons (*Columbia livia domestica*) by examining flight performance before and after removing measured lengths of either the innermost or outermost three primaries. All flight sessions were videotaped and took place in a large metabolic chamber, allowing for simultaneous measurement of flap rates, flight velocities, and metabolic rates. Simulated moult gaps of both types increased wing loading by approximately 10% and caused increases in flap rate and flight velocity of about 7% and 8% respectively. Metabolic rate was not significantly affected by the presence of simulated moult gaps. There was no detectable difference between the two moult-gap treatments with regard to aerodynamic or metabolic measurements. In general, the detrimental effects of moult gaps were minor, suggesting that the birds may be able to make biomechanical adjustments to compensate for the loss of wing area.

1. Introduction

Moult is a universal phenomenon in birds that has been shown to affect many aspects of avian physiology and behaviour, including metabolic rate (King 1980, Linström *et al.* 1993), thermoregulation (Shieltz & Murphy 1997), activity patterns (Newton 1966, Haukioja 1971, Ginn 1975), and flight ability (Tucker 1991, Chai 1997, Swaddle & Witter 1997). However, studies of the moulting process are generally lacking despite the relative importance of moult in the life histories of many bird species (Pyle *et al.* 1987), and the evolutionary forces underlying the origin and maintenance of moulting strategies are poorly understood. Information regarding the ecological costs and benefits of feather replacement is crucial in explaining the adaptive significance of the various moulting strategies practiced by birds.

Replacement of the primary feathers is perhaps the most critical aspect of moult as the primaries are generally the largest feathers (i.e. most energetically costly to replace) and are the most important for flight. In most birds primary moult proceeds from the innermost to the outermost primaries and takes place gradually such that only a few primaries are missing at the same time (Stresemann & Stresemann 1966, Ginn & Melville 1983). However, there are a number of notable exceptions to this general pattern. For example, parrots (Psittacidae) moult their primaries in two simultaneous waves that proceed proximally and distally from a focal point among the middle primaries (Forshaw & Cooper 1989), and almost all

waterfowl (Anseriformes) moult all of their primaries simultaneously leaving the birds temporarily flightless (Weller 1980).

It is likely that a number of ecological factors have influenced the pattern, timing, and intensity of primary moults (Stresemann & Stresemann 1966, Ginn & Melville 1983). Most considerations of the evolution of moulting strategies focus on time and/or energetic trade-offs wherein the moulting period is scheduled around other energetically expensive and time consuming activities such as breeding and migration (Cannell et al. 1983, Furness 1988, Weimerskirch 1991, Earnst 1992, Espie & James 1996, Langston & Rohwer 1996, Cobley & Prince 1998, Hemborg et al. 1998, Senar 1998, Filardi & Rohwer 2001). Less often considered is how moult may affect flight ability. An understanding of how the presence of moult gaps and their positions within a wing affect flight ability could provide new insights into the role of moult in avian life histories.

Despite the importance and ubiquity of moult in avian life histories, few have attempted to test the aerodynamic effects of flight-feather moult. Swaddle and Witter (1997) observed a decrease in level flight speed and take-off velocity in Starlings (*Sturnus vulgaris*) in association with trimmed wing feathers. They also found that gaps among the middle primaries caused the greatest change in flight speed; however, this treatment also entailed the greatest reduction in wing surface area. A computer model by Hedenström and Sunada (1998) suggested that wing gaps located near the middle of the wing (among the innermost primaries) are most detrimental in terms of lift curve slopes than gaps near the wing tip. Neither of these studies directly mentioned the effects of moult gaps on flight metabolic rates. However, it is intuitively straightforward to predict increases in metabolic rate in association with decreased mechanical flight efficiency.

In this experiment, I attempted to determine the biomechanical effects of wing moult on flight efficiency by observing the flight performance of pigeons (*Columbia livia domestica*) before and after experimentally trimming their primaries to simulate moult gaps (henceforth referred to as wing gaps). The study was designed to answer two questions: (1) how do gaps among the prima-

ries affect flight ability with regard to flight speed, flap rate and metabolic rate; and (2) do wing gaps in different positions have different effects on flight ability.

2. Materials and methods

2.1 The flight corridor/metabolic chamber

I measured a number of flight parameters in pigeons as they made short repeated flights in an airtight flight corridor similar to one described by Teal (1969). The corridor consisted of translucent, 6 mil polyethylene sheeting stretched over a wooden frame. In cross-section, the corridor was shaped like an upside-down triangle with a broad roof (1.08 m) and a narrow floor (9 cm). The corridor was 0.84 m in height and 13.3 m long, and contained an air volume of 7472.2 L. The width and shape of the corridor allowed for straight, unhindered flight and discouraged landing in the middle of the corridor. The floor was lined with copper wire and electrified to further discourage unwanted landings. Both ends of the corridor had a door and a flat landing surface also lined with wire. A small window at one end allowed for videotaping, and I installed a small fan beneath each landing platform to circulate the air within the corridor.

A Li-Core 6500 infrared gas analyser was attached to the middle of the apparatus to measure CO_2 accumulation. The gas analyser sampled the air in the chamber every 15 seconds via a tube with a flow rate of 1200 μmol/s. Sampled air was returned to the chamber through another tube. The gas analyser measured CO_2 concentrations with an error range of less than 0.5 ppm, and was calibrated before each day of use using a mixture of CO_2 at 700 ppm in N_2. Before the first flight session, I increased the corridor's CO_2 concentration to 726.7 ppm (approximately 325 ppm greater than the ambient CO_2 level) and observed a linear decrease to 718.0 ppm over 17.9 minutes, demonstrating that CO_2 leaked at a rate of –0.44 ppm/min. At the completion of all flight sessions, I retested the leak rate of the chamber and observed similar results — a decrease in CO_2 from 703.7 ppm to 691.6 ppm over 21.0 min (–0.57 ppm/min). Flight sessions lasted less than 10 minutes with

maximum CO_2 levels of less than 700 ppm (usually less than 500 ppm but dependent on ambient conditions and the amount of previous activity in the corridor) and with changes in CO_2 concentrations of between 60 and 110 ppm. Therefore, leakage of CO_2 from the chamber probably had little effect on my measurements.

I derived metabolic rates from increasing CO_2 levels in the chamber by fitting regression lines to plots of CO_2 concentration (ppm) versus time. I attempted to reduce uncertainties about CO_2 storage by the birds and mixing of gasses in the chamber by measuring CO_2 accumulation beginning two to three minutes after flights were initiated and lasting a minimum of three minutes during which there was a strongly linear increase in CO_2 concentration. The slopes of the regression lines gave CO_2 consumption rates for each flight session. Using the known volume of the chamber and the ideal gas law I converted CO_2 consumption to $\mu mol/h$, and I calculated flight metabolic rates using a fasting respiration quotient (RQ) of 0.707 such that 1 mMol CO_2/h = 0.1485 Kcal/h (Peters & Van Slyke 1946).

2.2 Flight Sessions

Experimental subjects were wild type Rock Doves raised in captivity and housed communally in a chicken coop with a small outdoor aviary. I monitored the birds' weights and adjusted their food intake to maintain constant body mass. Twelve birds were trained to fly from one end of the flight corridor to the other using lights at either end along with perches that could deliver an electrical shock. To compel a bird to fly I would illuminate the end of the flight corridor opposite the bird and subsequently deliver current to the bird's perch. Birds quickly began to respond to the light and would often fly without a negative stimulus. Each bird required two or three days of training before learning to fly directly from one perch to the other at regular intervals.

After training, each bird was subjected to three videotaped flight sessions in which I measured CO_2 concentration within the corridor at 15 s intervals. For each bird these three flight sessions were conducted within 40 min to 2 h of each other, to minimize confounding variables such as
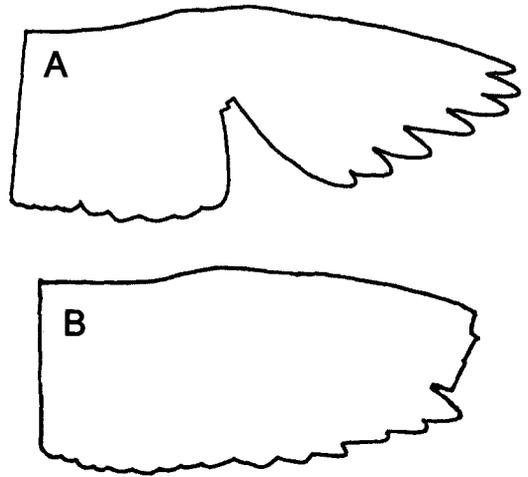
Fig. 1. Tracings of pigeon wings showing wing gaps produced by inner (A) and outer (B) primary trimming treatments.

changes in body mass or environmental conditions. On days when measurements were taken, focal birds were not fed until all three flight sessions were completed. Birds were compelled to make flights approximately every 20 s. Almost all flights were straight and uninterrupted with continuous flapping and with more intense flapping during the take-off and landing stages. Flights that did not adhere to this pattern were not used in calculating mechanical flight parameters. Each flight session lasted between 4 and 10 min depending upon the behaviour of the bird.

2.3 Flight-feather treatments

I employed two flight feather treatments, which consisted of trimming either the innermost or outermost three primaries. A length of 7 cm was trimmed from the tip of the most proximal of the three primaries (P1 or P8), with 8 and 9 cm removed from the next two primaries respectively (Fig. 1). I chose to use this feather-trimming scheme because it created gaps of equivalent size (surface area) among both inner and outer primaries and because I anticipated that it would make gaps large enough to induce measurable effects on flight. However, the gaps I made were larger than those that occur during natural wing moult in pigeons, and therefore may have amplified the effects of natural moult.

Because I could not repair trimmed primaries, I could not randomise the order of control and treatment flight sessions — control sessions had to come first. Therefore, I tested for carryover effects by randomly assigning half of the birds to undergo two control flight sessions prior to a single treatment session, whereas the other birds had one control session followed by two treatment sessions. Three birds from each of the two control/treatment schedules were assigned to each

treatment, to generate a two-by-two paired factorial design. To minimize handling between sessions, I measured and marked the feathers that were to be trimmed prior to the first recorded flight session. Immediately before each flight session I weighed the focal bird and photographed it with its left wing extended. These images were later digitised to determine the changes in wing surface area and wing loading caused by feather-trimming treatments.

Table 1. Treatments and measurements for individual birds are shown with each pre-treatment measurement listed above the italicized post-treatment measurement. Measures are averaged across two flight sessions when they are of the same type (control or treatment). The "Gap order" column presents the order of control (C) and treatment ("I" or "O") flight sessions with "I" and "O" signifying gaps among the inner and outer primaries respectively. Values in the "Difference" row are averages of the differences between control and treatment flight sessions for each bird with their 95% confidence intervals listed below.

Bird ID	Gap order	Mass (g)	Wing area (cm²)	Flight speed (m/s)	Flaps per s	M.R.* Kcal/ (h × kg)	No. of flights analyzed	Percent flight time
2	CII	410	300.7	3.35	7.14	59.2	22	21.1
		410	*271.6*	*3.82*	*7.72*	*47.0*	*35*	*18.8*
5	CCI	383	260.2	3.54	7.19	60.8	46	29.1
		386	*237.2*	*3.76*	*7.75*	*54.8*	*19*	*22.7*
7	CII	437	300.9	4.68	7.38	49.7	45	18.0
		430	*276.3*	*4.54*	*7.73*	*44.2*	*12*	*18.9*
10	CCI	425	287.4	4.61	7.27	44.5	34	15.3
		428	*263.7*	*4.63*	*7.85*	*39.8*	*26*	*15.0*
12	CCI	394	252.1	2.92	7.38	80.5	24	25.0
		391	*231.3*	*3.46*	*8.03*	*51.1*	*42*	*19.9*
18	CII	398	269.9	3.80	6.72	48.5	24	20.3
		390	*248.3*	*3.74*	*7.08*	*49.4*	*45*	*20.2*
1	CCO	407	277.6	3.00	7.18	57	33	24.5
		400	*253.3*	*3.29*	*7.50*	*60.1*	*19*	*22.9*
11	COO	403	311.1	4.01	6.85	–	17	15.7
		394	*284.8*	*3.87*	*7.33*	*–*	*11*	*14.2*
14	CO**	385	304.9	3.03	6.49	–	8	10.9
		405	*273.2*	*3.44*	*7.30*	*–*	*5*	*24.4*
15	COO	412	334.3	2.77	6.92	54.9	18	32.0
		405	*309.5*	*3.62*	*7.14*	*75.9*	*15*	*20.1*
16	COO	400	298.2	4.02	7.28	50.5	44	21.5
		401	*274.8*	*4.13*	*7.57*	*59.0*	*38*	*16.7*
17	CCO	406	259.8	3.76	7.22	53.9	41	18.5
		406	*233.2*	*4.22*	*7.89*	*47.3*	*23*	*16.3*
Mean		405	288.1	3.62	7.09	56.0	29.7	21.0
		404	*263.1*	*3.88*	*7.57*	*52.9*	*24.2*	*19.2*
Std Dev		15.3	24.7	0.64	0.28	9.99	12.6	5.98
		13.8	*23.4*	*0.43*	*0.31*	*10.28*	*13.1*	*3.20*
Difference		1.17	25.0	−0.25	−0.49	3.09		1.82
95% CI		±5.03	±1.93	±0.19	±0.11	±9.32		±3.75

*Mass specific metabolic rate
**Bird 14 had only one control session and one treatment session

2.4 Flight parameters and statistical tests

I derived overall flap rates for each bird by viewing each videotaped flight session in slow motion, counting the number of flaps for each uninterrupted flight, and dividing this count by the sum of the durations of the flights. Flights in which the bird went directly from one landing platform to the other were considered suitable. Average flight velocities were calculated for each bird by dividing the length of the flight corridor (13.3 m) by the mean flight duration. I estimated rates of CO_2 production by plotting the concentration of CO_2 in the flight corridor versus time. I then fitted a regression line to these data for each flight session and used the slopes of the lines as proxies for metabolic rate. Unless indicated otherwise, data were analysed using within-bird comparisons and two-tailed paired t-tests, thus eliminating problems associated with differences among individual birds. All means presented below are listed with associated standard errors.

3. Results

Measurements for each bird are summarized in Table 1. Wing gaps increased wing loading by 0.14 ± 0.006 g/cm^2 or $9.5 \pm 0.33\%$ with gaps among inner and outer primaries causing similar reductions in wing area ($t_{11} = 0.59$, P = 0.57). The mean difference in flap rate between successive flight sessions in which wing treatments were the same was 0.059 flaps/s and was not significantly different from zero ($t_9 = 1.05$, P = 0.32). Similar analyses of the number of flaps and the average flight velocity also had insignificant t-tests (flaps: $\bar{x} = 0.50$, $t_9 = 0.91$, P = 0.38; velocity: $\bar{x} = 0.10$, $t_9 = 1.5303$, P = 0.15). Thus, there is little evidence of carryover effects on any of these flight parameters, and in subsequent analyses, data from flight sessions with the same wing treatments were pooled.

The presence of wing gaps caused all but three birds to fly faster (Table 1), such that average flight velocity increased by $0.25 \pm .08$ m/s or $8.36 \pm 2.94\%$ ($t_{11} = 2.86$, P = 0.016), but there was no difference between changes in velocity caused by inner and outer flight feather treatments (two-tailed, unpaired t-test: $t_{11} = 0.86$, P = 0.41). Although flap rates (flaps per time) increased, wing gaps did not significantly change the mean number
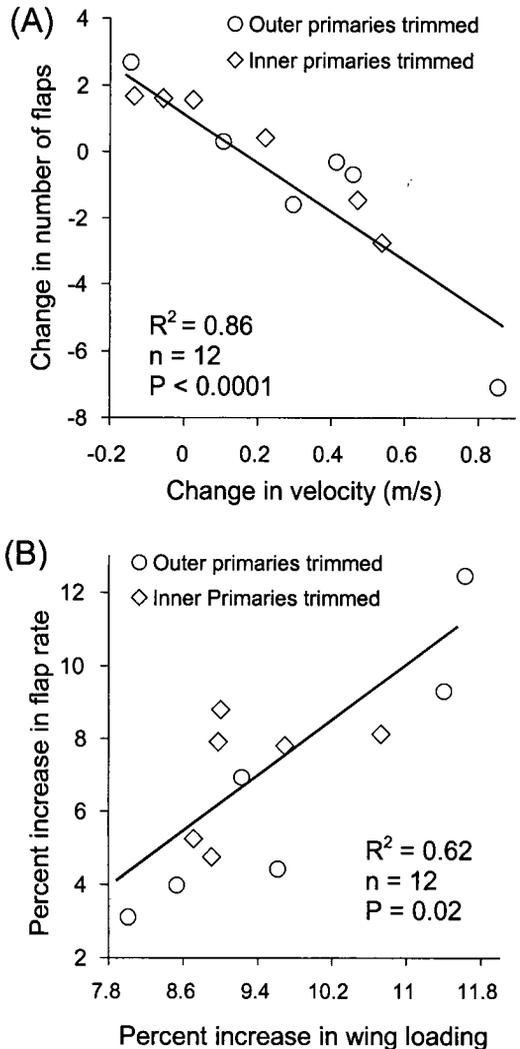
Fig. 2. Correlated flight parameters. (A) Changes caused by wing gaps in the number of flaps employed to complete a 13.3 m versus changes in average velocity. (B) Within-bird changes in flap rate versus changes in wing loading associated with wing-trimming treatments.

of flaps employed per 13.3 m flight ($t_{11} = 0.61$, P = 0.55), nor did the type of treatment affect the number of flaps (two-tailed, unpaired t-test: $t_{11} = 0.84$, P = 0.42). However, within-bird changes in the mean number of flaps per flight correlated negatively with changes in velocity ($R^2 = 0.86$, n = 12, P < 0.0001; Fig. 2a), indicating that birds which flew faster in response to wing trimming flapped less with respect to distance.
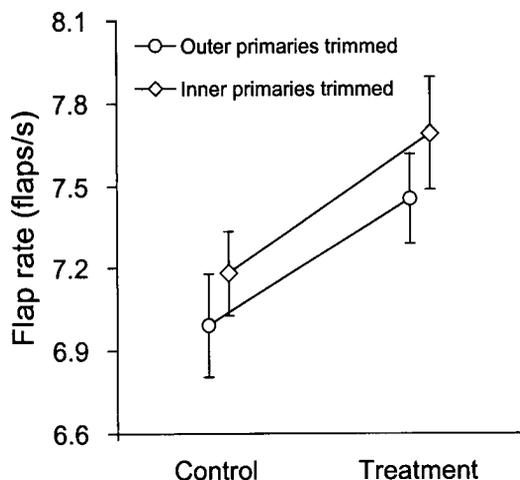
Fig. 3. Average flap rates for control and treatment flight sessions grouped by treatment type. n = 12 with six birds in each treatment type. Error bars denote 95% confidence intervals.

Wing trimming increased each bird's flap rate by an average of 0.49 ± 0.053 flaps/s or $6.9 \pm 0.8\%$ ($t_{11} = 8.88$, P < 0.0001; Fig. 3). Mean changes in flap rates associated with feather gaps did not differ between the two treatment groups (two-tailed, unpaired t-test: $t_{11} = 0.25$, n = 12, P = 0.81). A two-way ANOVA that included treatment type and the presence/absence of wing gaps as factors yielded a significant effect of treatment on flap rate (two way ANOVA: $F_{1,20} = 18.6$, P = 0.0003) but no interaction between inner and outer primary treatment types ($F_{1,20} = 0.044$, P = 0.84), indicating there was no effect on flap rate associated with the location of wing gaps (Fig. 3). The mean percent change in each bird's flap rate associated with wing trimming was correlated with the percent increase in wing loading ($R^2 = 0.62$, n = 12, P = 0.02; Fig. 2b) indicating that the flap rate measurements were sensitive enough to register the effects of slightly different wing gap sizes.

Because I was unable to collect CO_2 data for two birds (one in each treatment group), analyses of metabolic rates are limited to ten birds. Correlations of CO_2 concentration versus time were all highly significant (P < 0.0001), with R^2 values averaging 0.96 and ranging from 0.80 to 0.995. The birds averaged 21.9 ± 0.77 kcal/h for all flight sessions, and metabolic rate did not differ within each bird between paired flight sessions in which

wing treatments were the same ($t_7 = 1.68$, P = 0.14), indicating there was no carryover effect on metabolic rate. Grouping paired flight sessions and comparing control and treatment sessions within each bird, I found no effect of feather gaps (both gap types grouped together) on flight metabolic rate ($t_9 = -0.75$, P = 0.47). However, this analysis does not take into account that the proportion of time spent flying was slightly greater in control flight sessions than in treatment sessions ($t_9 = -2.97$, P = 0.016), reflecting the higher flight velocities observed when birds had wing gaps, and that the percentage of actual flight time was weakly correlated with rates of CO_2 production ($R^2 = 0.25$, n = 30, P = 0.005). Using a repeated-measures MANOVA that controlled for the effect of percent flight time and for differences among the birds, I still found no apparent effect of feather gaps on metabolic rate ($F_{1,10} = 1.74$, P = 0.23).

4. Discussion

Birds responded to wing gap treatments by increasing flap rates and flying faster. The observed increase in flight velocity associated with wing gaps contradicts the findings of Swaddle and Witter (1997), who observed decreased level flight velocity in European Starlings (*Sturnus vulgaris*) with experimentally trimmed flight feathers. However, because the amount of lift generated by a flying bird increases with airspeed when all other factors are held constant, (Pennycuick 1968), an increase in velocity may be necessary for a bird to maintain lift when its wing area is reduced.

There was no observable change in flight metabolic rate associated with wing gaps. This result may be due to the absence of an effect or lack of sensitivity in my measurement system. Although, my intention in measuring CO_2 production was not to empirically measure flight metabolic rate, but to compare metabolic activity between treatment and control flights, my data provide realistic estimates of metabolic rate associated with intermittent flight. My estimate of the average flight metabolic rate was very similar to LeFebvre's (1964) estimate of 21.5 ± 2.23 kcal/h for free flying pigeons which may have rested periodically. However, the birds in this study used less energy than birds that flew continuously in a

wind tunnel, which used 28.5 ± 0.38 kcal/h (Rothe *et al.* 1987), and birds in continuous free flight, which averaged 37.7 ± 1.83 kcal/h, (Gessaman & Nagy 1988).

Overall, the effects of wing gaps on flight parameters were surprisingly weak considering the degree to which wing loading was increased. However, it is possible that the birds responded to feather-trimming treatments by altering their flight behaviour in ways that would be difficult to detect. For instance, my measurements of wing surface area did not account for changes in wing shape that take place during the course of a flap cycle, and the birds could have spread their feathers more during the treatment flights, increasing their wing area to compensate for wing gaps. Furthermore, they may have increased the amplitude of their wing beats to provide more thrust. Although Figure 1b suggests a linear relationship between the increase in wing loading and reduction in flight ability, an exponentially increasing curve may be observed over a broader range of wing gap sizes as wing loading approaches a magnitude at which flight is no longer possible. The computer model of (Hedenström & Sunada 1998) offers similar predictions in that lift curve slopes (similar to lift to drag ratios) change little as wing gaps are expanded from 6.67% to 20% of the initial wing area.

Hedenström and Sunada (1998) also predicted that proximal wing gaps would be more detrimental than distal wing gaps. My data offer no support for this prediction in that there was no detectable difference between the effects of the inner and outer primary treatments. The reason for this disagreement may be due to the fact that Hedenström and Sunada conceived of a perfectly rectangular wing for their model rather than a more realistic wing shape, and this rectangular wing performed better when a distal wing gap was incorporated than it did with no wing gaps at all. Tucker's (1991) study of a moulting Harris' Hawk (*Parabuteo unicinctus*) trained to glide in a wind tunnel, agreed with my findings in demonstrating that the effects of wing gaps at the innermost and outermost primaries were equivalent. Tucker (1991) also observed that primary moult was most detrimental when the middle primaries were missing, a notion that I could not test because of sample size constraints.

Pigeons moult their flight feathers gradually such that there is rarely more than one primary missing at once (Johnston & Janiga 1995). Thus, the wing gaps I created were much larger than those that would result from natural primary moult. The surprisingly minor effects of these exaggerated wing gaps indicate that moult may not be a considerable detriment to sustained level flight. Nonetheless, most birds employ moulting strategies that appear to minimize the size of wing gaps at the expense of lengthening the moulting period (Voitkevich 1966, Payne 1972, Ginn & Melville 1983). The pervasiveness of gradual wing moult may be due to evolutionary pressure to maintain escape speed and agility rather than to mitigate the effects of moult on sustained flight (Swaddle & Witter 1997). However, energetic constraints are also likely to incur selective pressure for gradual primary moult in that a slow feather replacement rate allows a bird to spread out the energetic burden of feather generation (King 1974, Murphey & King 1992). As most of the flight parameters in this study were only slightly affected by wing gaps of robust size, my findings argue against the notion that most birds minimize the size of wing gaps solely to avoid compromising level flight efficiency.

It is important to note that the effects of wing gaps may vary with wing morphology and that birds with high wing loading will probably be more severely impaired by wing gaps. The effects of wing gaps may, in fact, help explain the evolution of the nearly simultaneous moult that occurs in high-wing-loading birds such as ducks (Anatidae) and auks (Alcidae) as a means of shortening the amount of time during which moult hinders flight (Welty 1982, Thompson *et al.* 1998). However, my results indicate that for the majority of bird species, moult-induced wing gaps are probably not a serious detriment to intermittent flight.

dations of "Guidelines for the Use of Animals in Research" (ASAB 1995) and were approved by the University of Minnesota Institutional Animal Care and Use Committee (Animal Subjects Code Number: 0004A9441).

Selostus: **Simuloidun käsisulkasadon vaikutus kyyhkysen lentoon**

Linnun sulkasato vaikuttaa muun muassa linnun käyttäytymiseen, aineenvaihduntaan, lämmönsäätelyyn, aktiivisuuteen ja lentokykyyn. Lintujen sulkasadon ja elinkierron ymmärtämisen kannalta on tärkeää arvioida siipisulkien vaihtamisesta aiheutuvia kustannuksia ja hyötyjä. Artikkelin kirjoittaja poisti kesykyyhkyltä tietyn mittaiset palat joko kolmesta sisimmästä tai kolmesta uloimmasta käsisulasta. Koelintujen (n = 12) lentoa videoitiin ennen ja jälkeen sulkien manipuloinnin aineenvaihduntakammiossa. Kullakin lintuyksilöllä tehtiin noin 30 lentosessiota ennen manipulointiaa ja 24 lentosessiota manipuloinnin jälkeen. Samanaikaisesti mitattiin kyyhkysen siiveniskujen määrää, siiveniskujen lyöntinopeutta ja aineenvaihduntaa. Käsisulkien manipulointi lisäsi siiven rasitusta noin 10 prosenttia. Siiveniskujen määrä kasvoi manipuloinnin myötä 7% ja linnun lentonopeus 8%. Siipien manipuloinnin ei sen sijaan havaittu vaikuttavan merkittävästi kyyhkyjen aineenvaihduntaan. Tulokset olivat samanlaisia riippumatta siitä, oliko manipuloitu sisimpiä vai uloimpia käsisulkia. Yleensä ottaen käsisulkien manipuloinnin haitalliset vaikutukset olivat vähäisiä. Oletettavasti linnut pystyvät kompensoimaan siiven pinta-alan menetystä biomekaanisin keinoin.

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