

# The effects of molt on the flight performance, body mass, and behavior of European starlings (*Sturnus vulgaris*): an experimental approach

John P. Swaddle and Mark S. Witter

**Abstract:** The physiological and energy costs of avian molt are well documented, but indirect consequences such as changes in flight performance have received less attention. Here, we report two experiments that investigated flight performance, body mass regulation, and behavior in captive starlings (*Sturnus vulgaris*). In the first experiment, we found a U-shaped change in take-off escape performance during natural molt: birds ascended at the shallowest trajectories during midmolt. Birds' body mass was also reduced during molt. In the second experiment, we manipulated the plumage of starlings to simulate different stages of flight-feather molt. This allowed us to separate the aerodynamic costs of feather loss from the physiological costs of feather synthesis normally associated with plumage growth. Through observations of flight (take-off, aerial maneuverability, and level flapping-flight speed) and behavioral parameters, we demonstrated that birds in simulated molt have reduced flight performance and reduced body mass. These birds also decrease the time spent performing energetically costly activities and seek areas of relative protection. In the longer term, some aspects of performance return to pretreatment levels, implying compensation for the plumage manipulations. Our results demonstrate that molt incurs significant functional costs that may play an important role in the adaptive radiation of molt strategies and molt patterns observed in avian species.

**Résumé :** Les coûts physiologiques et énergétiques associés à la mue chez les oiseaux sont bien connus, mais les conséquences indirectes de ces changements sur la performance de vol ont été moins étudiés. Nous avons procédé à deux expériences destinées à éprouver la performance du vol, le maintien de la masse corporelle et le comportement chez des Étourneaux sansonnets (*Sturnus vulgaris*) en captivité. La première expérience a démontré l'existence d'un changement en forme de U dans la performance d'envol au cours de la mue naturelle; les oiseaux ont pris leur envol selon les trajectoires le moins arquées vers le milieu de la mue. Les oiseaux ont également subi des pertes de masse au cours de la mue. Dans la seconde expérience, nous avons manipulé le plumage des oiseaux de façon à simuler les différentes stades de la mue des rémiges. Cette expérience nous a permis de distinguer les coûts aérodynamiques de la perte des plumes des coûts physiologiques de la synthèse des plumes normalement associés à la croissance des nouvelles plumes. Par observation du vol (envol, manoeuvrabilité aérienne, vitesse du vol par battement des ailes) et des paramètres du comportement, nous avons constaté que les oiseaux à mue simulée ont une moins bonne performance de vol et une masse corporelle réduite. Ces oiseaux diminuent également leurs activités à coût énergétique élevé et recherchent les endroits où ils peuvent trouver une protection relative. À long terme, certains aspects de la performance redeviennent normaux, ce qui suppose que les oiseaux compensent la manipulation du plumage de quelque façon. Nos résultats démontrent que le mue comporte des coûts fonctionnels significatifs qui peuvent jouer un rôle important dans la radiation adaptative des stratégies de mue et des patterns de mue observés chez les espèces d'oiseaux.

[Traduit par la Rédaction]

## Introduction

Molt is a crucial and energetically demanding stage in the annual cycle of many birds. It involves the replacement of feathers that can constitute up to 30% of lean dry body mass (Jenni and Winkler 1994). The physiological and metabolic costs associated with feather replacement are well documented (see Payne 1972; Murphy et al. 1990; Murphy and King 1992; Lindström et al. 1993). However, the flight

performance costs associated with feather loss are less well characterized. There are numerous reports of molting birds exhibiting less conspicuous behavioral patterns (Newton 1966; Haukioja 1971a; Ginn 1975) and even flightlessness in some species (Sullivan 1965; Stressemann and Stressemann 1966; Haukioja 1971a, 1971b). However, to date there has been only one direct study of the flight effects of flight feather molt (Tucker 1991) and no controlled study of the ecological consequences of feather molt in any species. Assessments of the functional consequences, along with the known physiological and energy changes that occur during molt, are vital in explaining the adaptive significance of molt strategies and patterns (see Jenni and Winkler 1994; Holmgren and Hedenström 1995).

In this study we investigated the effects of both natural molt and simulated stages of flight-feather molt (early, mid, and late stages of molt) on body mass, behavior, and eco-

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J.P. Swaddle<sup>1</sup> and M.S. Witter. Division of Environmental and Evolutionary Biology, Institute of Biomedical and Life Sciences, Graham Kerr Building, University of Glasgow, Glasgow, G12 8QQ, United Kingdom.

<sup>1</sup> Author to whom all correspondence should be addressed (e-mail: gbza86@udcf.gla.ac.uk).

logically relevant parameters of flight performance in the European starling (*Sturnus vulgaris*). Molt is well documented in this species (e.g., Bährmann 1964; Feare 1984; Ginn and Melville 1983; Swaddle and Witter 1994) and the adult molt appears to be typical of most European passerines (Feare 1984). By simulating different stages of primary and tail feather molt through experimental manipulation of the flight plumage, we are able to separate the functional aspects of feather loss from the physiological and metabolic changes that occur naturally during molt. In this way, we are able to test directly whether disruption of the flight surface influences behavior and flight performance independently of the underlying physiological changes associated with molt. We have assessed the influence of the simulated stages of feather molt on four different aspects of flight: angle of take-off, speed of take-off, aerial maneuverability (defined in this experiment as the ability to negotiate an obstacle course, so incorporating elements of both maneuverability and agility; refer to Witter et al. 1994; Swaddle et al. 1996), and level-flight speed. These flight parameters are likely to influence aspects of individual fitness (e.g., predator avoidance) and so may be optimized by natural selection (see Lima 1993; Witter et al. 1994). For example, many avian species rely on a short escape flight to cover to evade predation (e.g., Grubb and Greenwald 1982; Lindström 1989; Lazarus and Symonds 1992). Both the speed and trajectory of take-off have been suggested as important determinants of predation risk (Page and Whitacre 1975; Kenward 1978; Cresswell 1993; Witter et al. 1994; Metcalfe and Ure 1995). Once potential prey are airborne, maneuverability and agility may be of primary importance in evading predation (see Rudebeck 1950; Bijlsma 1990; Cresswell 1993), and are also likely to be highly related to the ability to negotiate crowded habitats (e.g., woodlands) without suffering wing damage.

Through these experiments we are able to examine a number of hypotheses relating to avian molt. We examine whether disruption of the flight surfaces results in impaired flight performance. Impaired flight performance during natural molt may be associated with, for example, atrophied flight musculature or depleted energy reserves (e.g., Piersma 1988), in addition to changes in the flight surfaces. By manipulating plumage directly, we are able to examine specifically the role of flight surface disruption. We investigate changes in body mass associated with simulated molt. The changes in body mass associated with natural molt have often been explained in terms of the physiological and energy demands of feather synthesis (e.g., Chilgren 1977; Newton 1968; Lindström et al. 1993). By simulating molt through plumage manipulations we can examine changes in body mass associated only with alterations in plumage (cf. Witter and Cuthill 1993). Similarly, changes in behavior associated with natural molt have been attributed to changing energy and nutritional requirements and increased predation risk (Newton 1966; Haukioja 1971a; Jenni and Winkler 1994). Here we examine changes in behavior associated only with flight-plumage manipulations, removing requirements associated with feather synthesis.

## Method

### Natural molt

We performed the first experiment on 8 wild-caught adult male starlings with undamaged flight plumage that were housed in out-

door aviaries (3 × 3 × 2 m) under natural photoperiod. Birds were provided ad libitum with food, drinking water, and bathing water throughout a natural molt (June to October) and housed in accordance with the guidelines of the Canadian Council on Animal Care. On five occasions during this period, we caught the birds and measured the following: body mass (to 0.1 g on an electronic balance, controlling for the effects of time of day), primary molt score for the left wing (0–45; Ginn and Melville 1983), and the length of each growing primary on the left wing (to 0.01 cm with vernier calipers; primary length was defined as the distance from the point of feather insertion into the skin to the distalmost point of the feather tip). In a separate procedure, we recorded the escape take-off behavior (see Witter et al. 1994) of each bird. Take-off was assessed in a long narrow aviary (1 × 2 × 4 m). Half of the aviary was open space; the other half was filled with dense vegetation, shrubs, and perches (protective cover). Birds were released, at the open end of the aviary, from a perch positioned 5 cm above the ground, simultaneously with the sounding of a loud vocal startle stimulus; hence, the birds exhibited an "escape" response. Birds had to ascend over an opaque barrier 1.2 m high, 1.5 m from the perch, to reach the area of cover. Take-offs were recorded on Hi-8 video tape (Sony CCD-TR707E) at a shutter speed of 1/200 s and frame rate of 25 frames/s, the camera being placed perpendicular to the line of flight in a level horizontal plane. The videotapes were subsequently analyzed (using frame-by-frame playback on a Sony EV-2000E) and digitized (on a Macintosh 7500AV computer, using the public domain NIH Image program) to derive measures of trajectory and speed. Specifically, we measured the mean angle of ascent in flight (the angle subtended at the position of the bill tip when the bird was first in flight from the position of the bill tip after approximately 0.2 s of flight) and flight speed after 0.2 s of flight (speed, calculated from the total distance moved during three consecutive frames of the video after 0.2 s of flight). We used these data to examine the natural changes in take-off performance, body mass, and primary lengths during an unmanipulated molt.

### Simulated molt

#### Plumage manipulations

We performed the experiment on 45 nonmolting adult starlings of both sexes with undamaged flight plumage. Birds were housed in an outdoor aviary (5 × 3 × 2 m), provided ad libitum with food and water, and housed in accordance with the guidelines of the Canadian Council on Animal Care. We randomly allocated 9 birds to each of five experimental treatment groups, as follows. (1) Early: fine scissors were used to reduce the length of primary 1 (the most proximal primary feather) to 6.5 cm, primary 2 to 5.0 cm and primary 3 to 0.5 cm. Tail feather 1 (the innermost) was reduced to 0.5 cm. This simulated an early stage of flight-feather molt, equivalent to a primary molt score of 8. (2) Mid: primary 4 was reduced in length to 6.0 cm, primary 5 to 4.5 cm, and primary 6 to 0.5 cm. Tail feather 3 was reduced to a length of 0.5 cm. This manipulation typified the midstage of flight-feather molt, equivalent to a primary molt score of 23. (3) Late: primary 6 was reduced to 8.5 cm, primary 7 to 5.5 cm, and primary 8 to 0.5 cm. The outermost tail feathers were reduced in length to 0.5 cm. This manipulation simulated feather lengths typical of those observed during late stages of molt, equivalent to a primary molt score of 33. Primary 9 (the distalmost) was not manipulated, as shortening of this feather may have directly influenced the efficacy of our measure of aerial maneuverability (see below). (4) Control I: birds were handled for the same amount of time as those in the other experimental treatments, but the plumage was not manipulated. (5) Control II: the feather tips (approximately 0.2 cm) of primaries 6, 7, and 8 and those of the outermost tail feather were removed. This second control treatment was included to test for nonspecific effects of feather trimming. Before and after the plumage manipulations, flattened wing tracings at maximum wing spread were taken from

each bird to calculate wing area not including body area. One week before, immediately following, and 2 weeks after the manipulations were performed, we recorded take-off performance and aerial maneuverability of the birds. Following this period, we examined the influence of the manipulations on level-flight speed and behavior. These procedures are detailed below.

#### *Take-off performance*

The trajectory and speed of escape flights were assessed in a long narrow flight aviary ( $3.5 \times 1.2 \times 2$  m) separate from the aviary used in the natural molt experiment. One end of this aviary contained perching sites, food, drinking water, and bathing water. The opposite end of the aviary was empty except for a single perch positioned 5 cm above the ground, from which birds were released, after being weighed (to 0.1 g accuracy) on an electric balance. A 1.2 m high opaque barrier was placed across the inside of the aviary, 1.5 m from the take-off perch. Birds were released at the open end of the aviary from the perch and simultaneously exposed to a loud vocal startle stimulus. All birds ascended immediately from the perch, over the barrier, to the end of the aviary containing perching sites. The take-offs were recorded on Hi-8 videotape with a video camera (Sony CCD-FX700E) at a shutter speed of 1/4000 s, the camera being placed perpendicular to the line of flight. The videotapes were subsequently analyzed and digitized as described above.

#### *Aerial maneuverability*

Performance through an aerial maneuverability testing course was assessed in the same flight aviary used for the take-off analysis of simulated molt. The opaque barrier was removed and wooden poles covered in waterproof parcel tape were suspended from the aviary ceiling in ordered rows. Poles hung in a vertical plane. There were five rows of poles with alternately three and four poles per row in a staggered arrangement (cf. Witter et al. 1994). Within rows, poles were 0.3 or 0.25 m apart. Rows were 0.25 m apart. For each bird, the tips of the distalmost primaries from both wings were dipped in a small standardized volume of water-soluble black ink. Birds were released from a perch approximately 1.5 m above the floor at the open end of the course and simultaneously exposed to a loud vocal startle stimulus. All individuals flew directly through the course to the opposite side of the aviary. We recorded the number of rows that each individual made contact with (displayed by ink marks on the poles; cf. Witter et al. 1994; Swaddle et al. 1996). As for the take-off analysis, body mass was recorded (to 0.1 g accuracy) on an electronic balance before each trial.

#### *Level flight*

Measurements of level-flight speed were assessed 3 weeks after we performed the plumage manipulations. We allowed birds to fly freely along a long flight corridor (approximately  $14 \times 1.5 \times 2.5$  m) between perches placed at either end 1.5 m above the floor. A video camera (as above) was placed perpendicular to the line of flight and was focused on the central 2-m section of the corridor. We subsequently analyzed the videotapes to measure level-flight speed. We ignored all flights in which the birds were seen to ascend, descend, or turn while flying across the field of view. Turning flight was identified by the posture of the birds in flight on the video recordings and by our direct observations during flight trials. Ascent and descent were defined as changes of more than 10 cm in the vertical location of the birds during the flight across the field of view. Thus, we only recorded speed from straight level flights. We measured speed from the distance the birds flew over three consecutive frames of the videotape, using the digitizing procedure described in the first experiment. We took the mean speed from the first four separate flights that satisfied our criteria for straight level flight for each bird. Body masses were also recorded immediately before each flight session as described above. By this stage of the experiment, a few of the birds had suffered

noticeable primary and tail feather damage and so sample sizes in the manipulation groups were reduced to the following: 9 for control I, 7 for control II, 7 for early, 8 for mid, and 7 for late.

#### *Behavior*

Immediately following the level-flight experiment, we randomly allocated quintets of birds to seven flight aviaries (measuring  $3 \times 2 \times 2$  m). One bird from each of the five treatment groups was represented in each aviary. Aviaries were identical; each contained areas of cover, multiple perching sites at variable heights, and ad libitum food, drinking water, and bathing water. After birds had spent 4 days in these aviaries, time and location budgets were recorded for each bird using a focal-animal sampling technique. We recorded six activity variables and three location variables. We calculated time spent in each of the following mutually exclusive activities: (i) feeding, including probing for food, at the feeding dishes and elsewhere; (ii) nonflying locomotory activity, including walking and running on the ground and hopping between perches; (iii) self-maintenance preening and bill wiping; (iv) vocalizing; (v) social interactions, including aggressive posturing (see Feare 1984) and direct aggressive contact; (vi) no observable activity. We calculated time spent in each of the following locations: (i) ground, principally the floor of the aviary but also food and water dishes that were located on the floor; (ii) perches, including wooden perches, natural vegetation, and the side-netting of the aviaries, but excluding food and water dishes; (iii) air. The location variable "air" is directly equivalent to time spent in flight, and so might be considered a seventh activity variable. Each bird was observed during one 10-min observation period. The order of observations of each bird in each aviary was randomized to eliminate systematic order biases between treatments. All observations were made between 11:00 and 14:00 over 3 consecutive days.

#### *Statistical analyses*

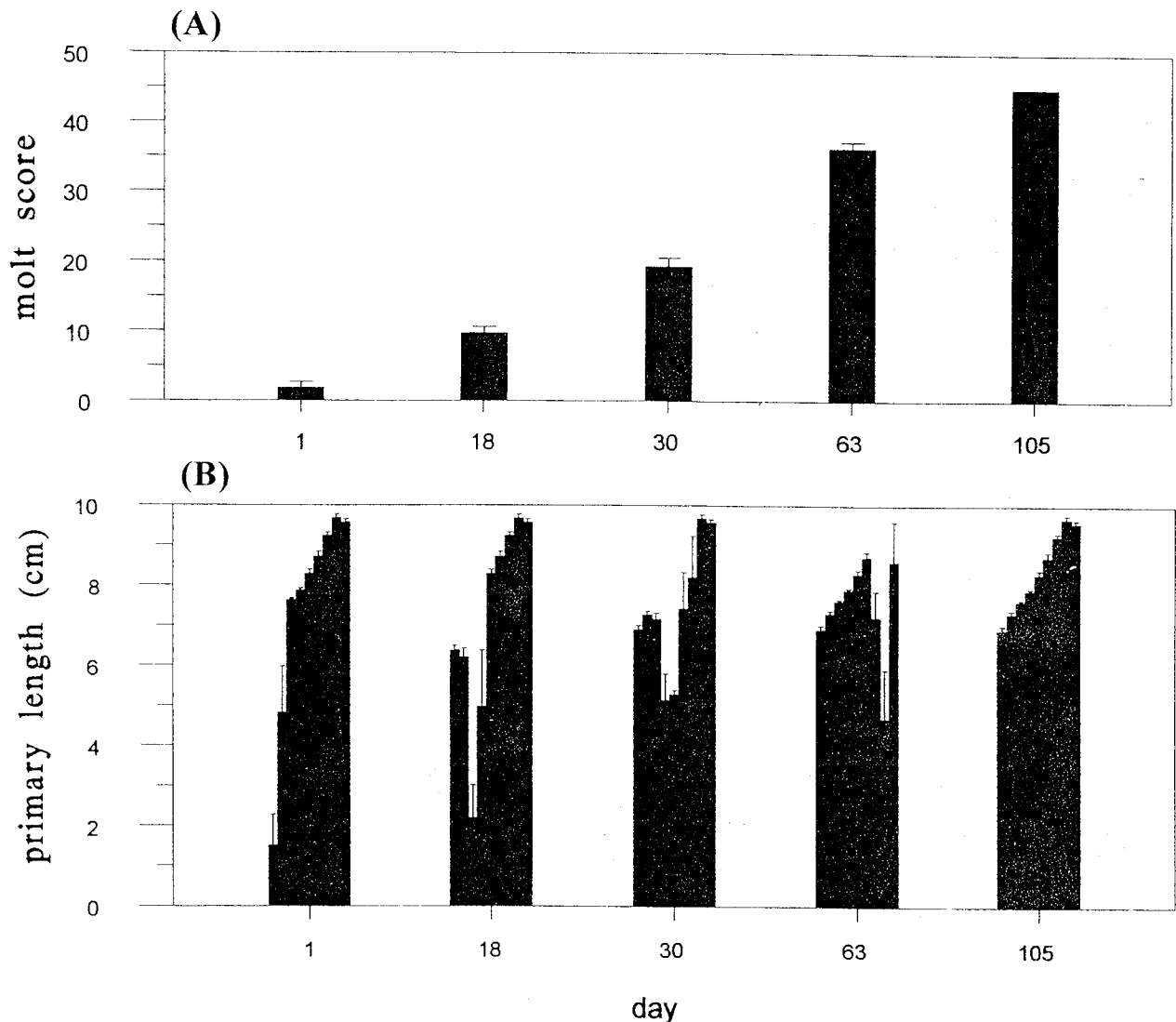
We analyzed all take-off and maneuverability data using the MANOVA procedure on SPSS (SPSS Inc. 1988). The natural molt analysis comprised a within-subjects effect "time" (day during molt). The simulated molt analysis comprised a within-subject factor "time" (the day in the experiment) and a between-subjects factor "group" (the treatment group from which the birds came). These analyses were performed both with and without body mass as a covariate (see Results). Wing area, body mass, and wing loading were analyzed similarly, except that body mass was not entered as a covariate. Level-flight and behavioral analyses were performed on MINITAB (Minitab Inc. 1994). The level-flight analysis comprised a one-way analysis of variance (ANOVA) with the factor "group." As no convenient transformations normalized behavioral data, these were analyzed nonparametrically (see Siegel and Castellan 1988). For the behavioral analyses, we treated each aviary, rather than each bird, as an independent datum to avoid pseudoreplication (Hurlbert 1984). This was achieved using a Friedman's ANOVA, blocked by aviary, treating treatment groups as repeated measures within each aviary. Differences between treatment groups were investigated using an orthogonal pairwise contrast matrix or orthogonal polynomial contrasts (see Hand and Taylor 1987). The orthogonal contrast matrix comprised the following comparisons: (i) control I and control II vs. early, mid, and late; (ii) early vs. late; (iii) mid vs. early and late; (iv) control I vs. control II. Two-tailed tests of probability are used throughout and all values are shown as the mean  $\pm$  SE unless otherwise stated.

## **Results**

### *Natural molt*

The molt scores and primary lengths for the birds during each of the flight sessions are shown in Fig. 1. Body mass changed significantly during molt ( $F_{[4,28]} = 8.71$ ,  $P <$

Fig. 1. Mean (+ SE) molt scores (A) and primary lengths (B) for all birds in each measurement session during natural molt. Primaries are shown from the innermost to the outermost from left to right within days. Day 1 refers to the day of the first measurement session.



0.001), being at its lowest during midmolt and its highest at the end of molt (Fig. 2A). Birds exhibited a significant U-shaped change in the initial angle of ascent in flight during molt: initial angles of ascent were highest at the beginning and end of molt ( $F_{[4,28]} = 7.53$ ,  $P < 0.001$ ; quadratic polynomial contrast,  $t = 3.82$ ,  $P = 0.007$ ; other contrast terms,  $t < 1.524$ ,  $P > 0.171$ ; Fig. 2B). Escape-flight speeds did not differ significantly during molt ( $F_{[4,28]} = 1.44$ ,  $P = 0.247$ ; Fig. 2C).

### Simulated molt

#### Wing area, body mass, and wing loading

The manipulations significantly affected changes in wing area ( $F_{[4,40]} = 730.89$ ,  $P < 0.0001$ ; Fig. 3A). Changes in wing area did not differ significantly between early- and late-molt treatments, but both early- and late-molt manipulations resulted in smaller reductions in wing area than mid-molt birds (Fig. 3). The manipulations of flight plumage resulted in marked changes in body mass ( $F_{[4,40]} = 3.75$ ,

$P = 0.011$ ; Fig. 3B). Body mass of birds that underwent molt-simulation treatments was reduced relative to that of the control birds. There were no significant differences in mass either between the control groups or among the three experimental groups (Fig. 3).

Change in wing loading (body mass divided by wing area) also differed significantly with treatment group between the day of manipulation and 2 weeks later ( $F_{[4,40]} = 4.69$ ,  $P = 0.003$ ; Fig. 3C). Birds in the mid-molt treatment, where wing area was reduced the most, suffered the largest increase in wing loading. The other groups did not differ significantly (Fig. 3). Thus, although body mass of the molt-simulation birds was reduced following the manipulation, it was not enough to compensate for the decrease in wing area experienced by the mid-molt birds, but did so in the early- and late-molt birds.

#### Take-off

There was no effect of the manipulations on angle of take-off, measured immediately after the manipulations ( $F_{[4,39]} =$

1.16,  $P = 0.342$ ; Fig. 4A), but there was an effect on the speed of take-off ( $F_{[4,39]} = 3.30$ ,  $P = 0.020$ ; Fig. 4B). Birds with simulated stages of primary and tail molt flew slower during take-off than control birds, and early-molt birds took off more slowly than birds in late molt. There were no other significant differences between groups (see Fig. 4). To examine the occurrence of any compensational changes the birds may have undertaken in response to the manipulations, take-off measures recorded 1 week before the manipulations were also compared with those taken 2 weeks after the feather manipulations. These analyses indicated that there was no subsequent change in take-off angle but there was a compensational response in take-off speed, take-off speed being restored to pretreatment levels after 2 weeks (Fig. 4).

To examine whether this compensational response may have occurred through the changes in body mass, we examined the ANOVA model without body mass entered as a covariate. This did not alter the results: take-off speed was still affected by the manipulations immediately after they were performed ( $F_{[4,40]} = 3.58$ ,  $P = 0.014$ ; orthogonal contrasts, control I and control II vs. early, mid and late,  $t = 2.670$ ,  $P = 0.011$ ; early vs. late,  $t = 2.290$ ,  $P = 0.0270$ ; other terms,  $t < 1.17$ ,  $P > 0.24$ ), but this effect was no longer present 2 weeks after the manipulations ( $F_{[4,40]} = 0.49$ ,  $P = 0.741$ ). This indicates that change in body mass alone does not fully account for the compensational response observed. Angle of take-off was also unaffected by removal of body mass from the analysis: there was still no relation between angle of trajectory and molt category either at the time of manipulation ( $F_{[4,40]} = 1.77$ ,  $P = 0.153$ ) or 2 weeks later ( $F_{[4,40]} = 1.12$ ,  $P = 0.362$ ).

#### Aerial maneuverability

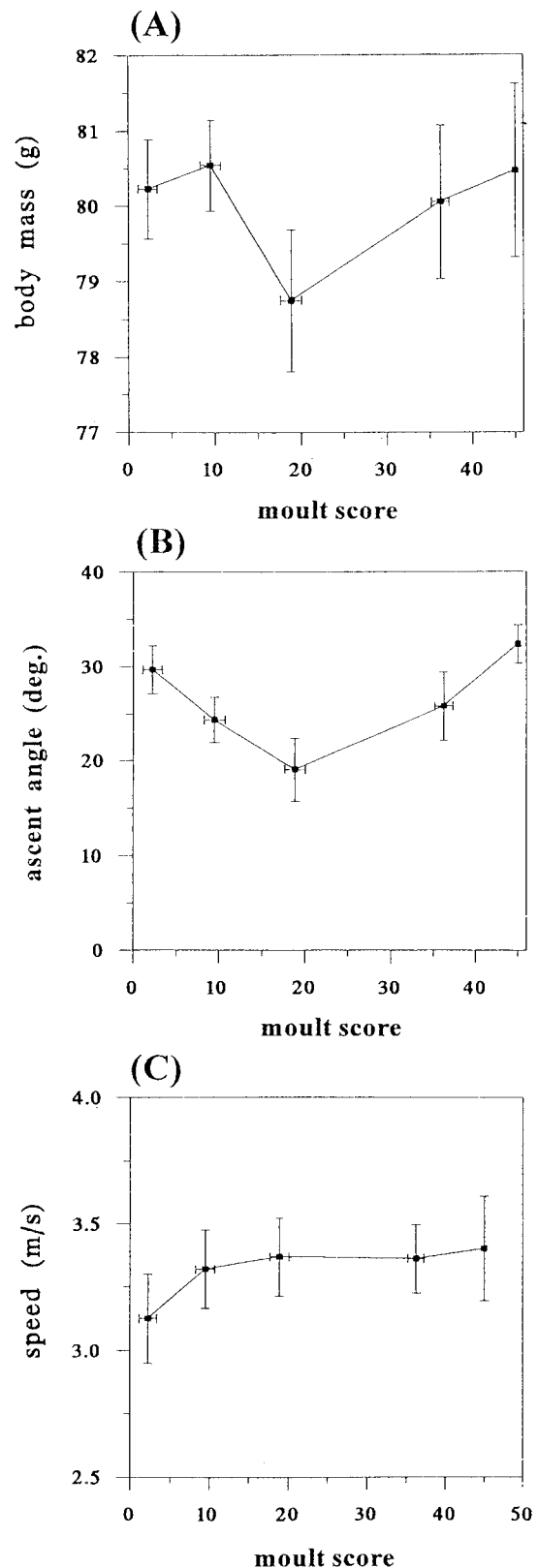
The molt-simulation treatments reduced flight performance through the maneuverability testing course immediately following the manipulations (Fig. 5). The molt-simulation treatments made contact with more rows than the control treatments, but there were no significant differences between the stages of molt (Fig. 5). The birds in the molt-simulation treatments appeared to compensate for the manipulations, as there were no differences in maneuverability between treatment groups 2 weeks after the manipulations were performed ( $F_{[4,39]} = 0.49$ ,  $P = 0.742$ ).

As in the take-off analyses, the between-group changes in body mass do not fully explain these compensations. When body mass is removed from the ANOVA model, the same patterns of change in maneuverability are observed, both at the time of manipulation ( $F_{[4,40]} = 2.89$ ,  $P = 0.034$ ; orthogonal pairwise contrasts, control I and control II vs. early, mid, and late,  $t = 3.137$ ,  $P = 0.003$ ; early vs. late,  $t = 0.174$ ,  $P = 0.863$ ; mid vs. early and late,  $t = 1.303$ ,  $P = 0.200$ ; control I vs. control II,  $t = 0.001$ ,  $P = 0.999$ ) and 2 weeks later ( $F_{[4,40]} = 0.512$ ,  $P = 0.727$ ).

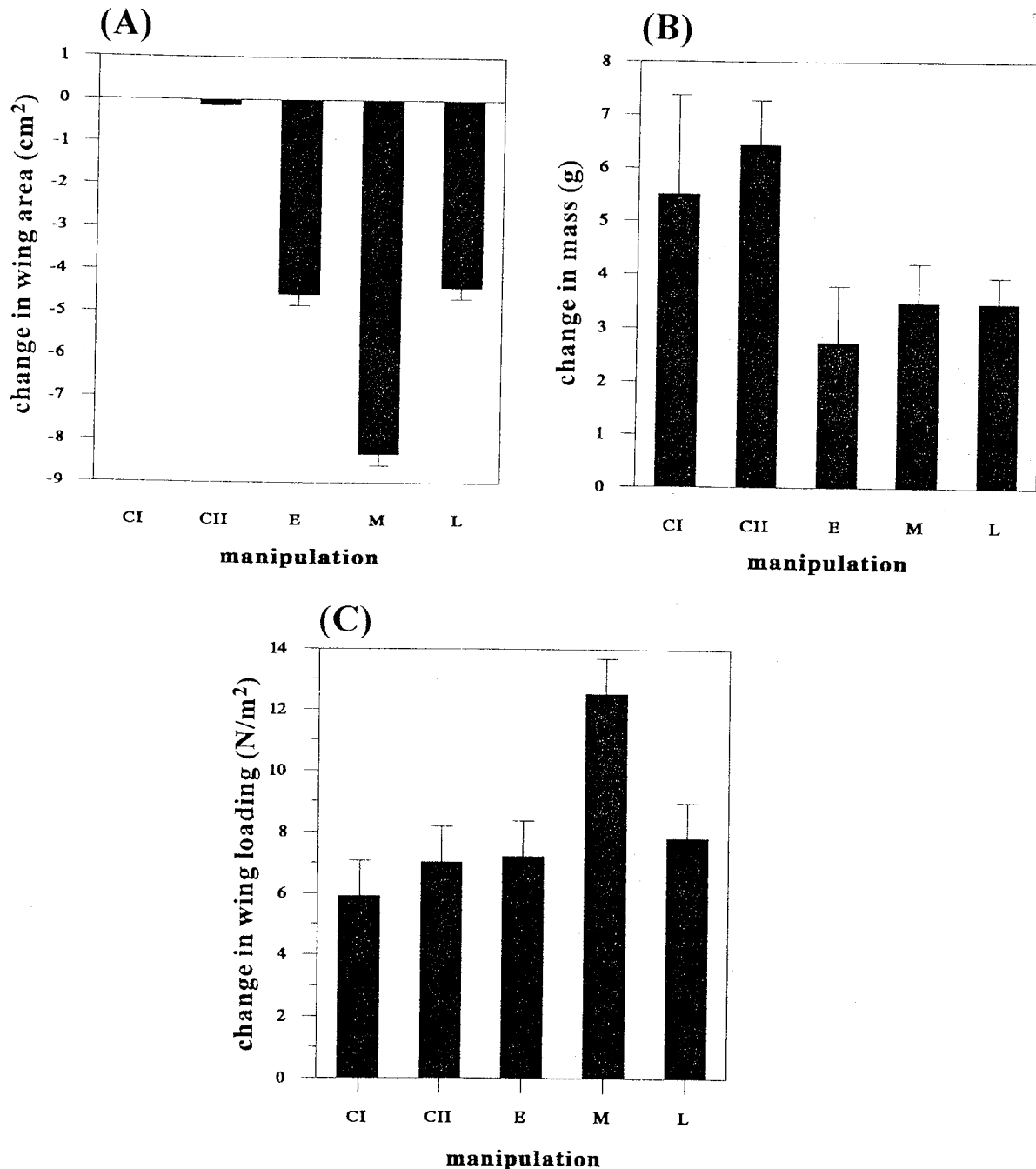
#### Level flight

The manipulations significantly affected level-flight speed, both when body mass was entered into the analysis as a covariate ( $F_{[4,32]} = 5.92$ ,  $P = 0.001$ ; Fig. 6) and when it was excluded ( $F_{[4,33]} = 6.81$ ,  $P < 0.001$ ). Birds in the molt-simulation treatments flew more slowly than controls ( $t = 5.09$ ,  $P < 0.0001$ ), but there were no significant differ-

**Fig. 2.** Mean ( $\pm$  SE) body mass (A), initial angle of ascent (B) in flight; and speed (C) during take-off versus stage of molt, represented as mean ( $\pm$  SE) molt score, for each of the five measurement sessions during natural molt. For an explanation of treatment groups see Fig. 1.



**Fig. 3.** Mean (+ SE) change in wing area (A) due to the molt-simulation treatments, change in body mass (B), and change in wing loading (C) versus treatment group between the day of manipulation and 2 weeks after the manipulation. All three variables changed significantly as a result of the manipulations. Wing area:  $F_{[4,40]} = 730.89$ ,  $P < 0.0001$ ; orthogonal contrasts, control I (CI) and control II (CII) vs. early (E), mid (M), and late (L),  $P < 0.0001$ ; early vs. late,  $P = 0.660$ ; mid vs. early and late,  $P < 0.0001$ ; control I vs. control II,  $P < 0.001$ . Body mass:  $F_{[4,40]} = 3.75$ ,  $P = 0.011$ ; orthogonal contrasts, control I, and control II vs. early, mid, and late,  $P = 0.0095$ ; early vs. late,  $P = 0.641$ ; mid vs. early and late,  $P = 0.781$ ; control I vs. control II,  $P = 0.553$ . Wing loading:  $F_{[4,40]} = 4.69$ ,  $P = 0.003$ ; orthogonal contrasts, control I, and control II vs. early, mid, and late,  $P = 0.016$ ; early vs. late,  $P = 0.716$ ; mid vs. early and late,  $P = 0.001$ ; control I vs. control II,  $P = 0.513$ .



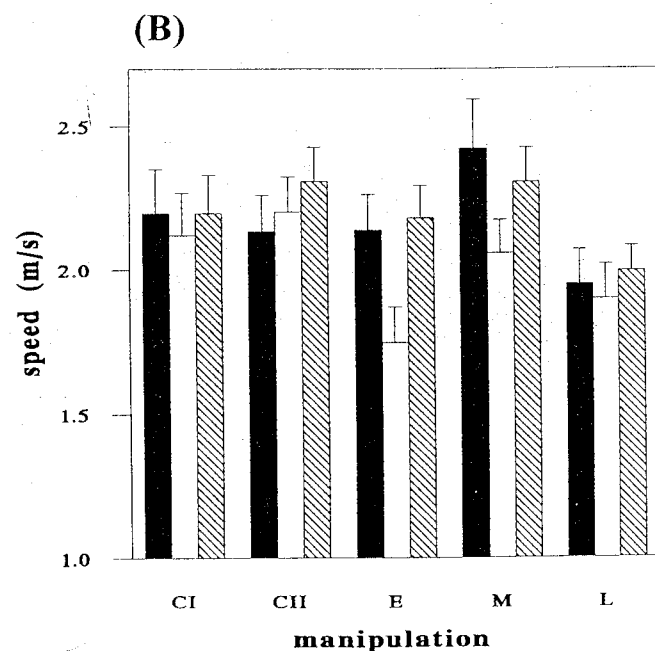
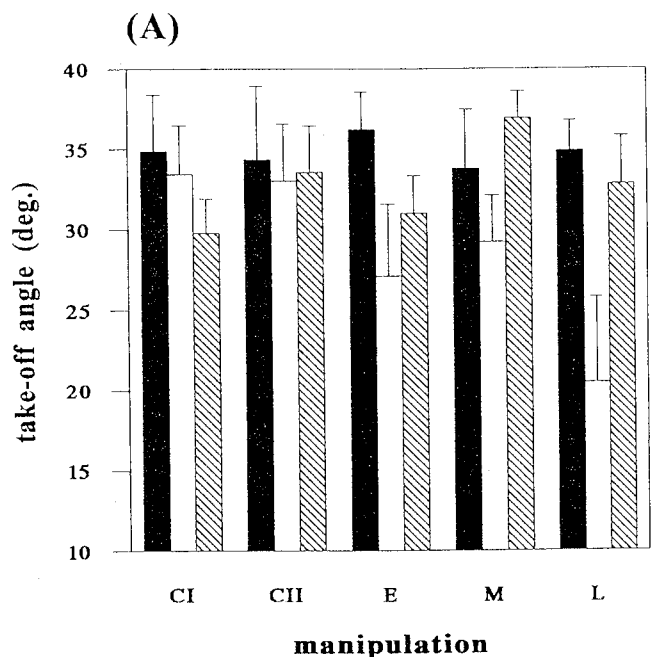
ences between stages of molt ( $t < 1.60$ ,  $P > 0.13$ , in all cases) or between control treatments ( $t = 0.10$ ,  $P = 0.93$ ).

#### Behavior

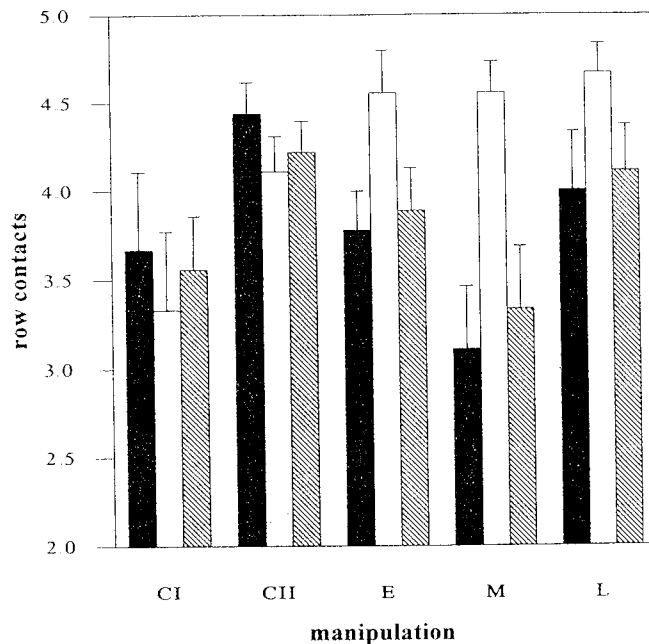
The plumage manipulations significantly influenced the time birds spent in particular locations (Fig. 7) and activities

(Fig. 8). Birds in simulated stages of molt spent more time perching ( $S = 14.40$ ,  $df = 4$ ,  $P = 0.006$ ; Fig. 7A) and less time in the air ( $S = 11.43$ ,  $df = 4$ ,  $P = 0.023$ ; Fig. 7B) than controls. For both variables, there were no significant differences between the three stages of molt or between control treatments (see Fig. 7). Manipulated birds tended to spend

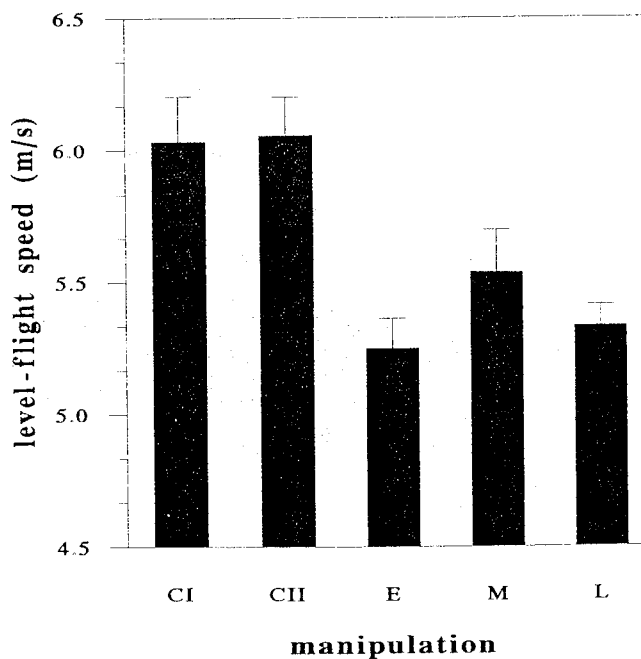
**Fig. 4.** Mean (+ SE) initial angle of ascent (A) and speed (m/s) of escape take-off versus molt simulation group. Solid bars represent measures taken 1 week before, open bars measures taken immediately after, and hatched bars measures taken 2 weeks after the plumage manipulations. When data from before and immediately after the manipulations were compared, angle of take-off was unaffected ( $F_{[4,39]} = 1.16, P = 0.342$ ), but speed changed ( $F_{[4,39]} = 3.30, P = 0.020$ ; orthogonal contrasts, control I and control II vs. early, mid, and late,  $P = 0.023$ ; early vs. late,  $P = 0.030$ ; mid vs. early and late,  $P = 0.175$ ; control I vs. control II,  $P = 0.672$ ). When data from before and 2 weeks after the manipulations were compared, neither angle nor speed differed significantly by treatment group (angle,  $F_{[4,39]} = 1.07, P = 0.385$ ; speed,  $F_{[4,39]} = 0.83, P = 0.513$ ).



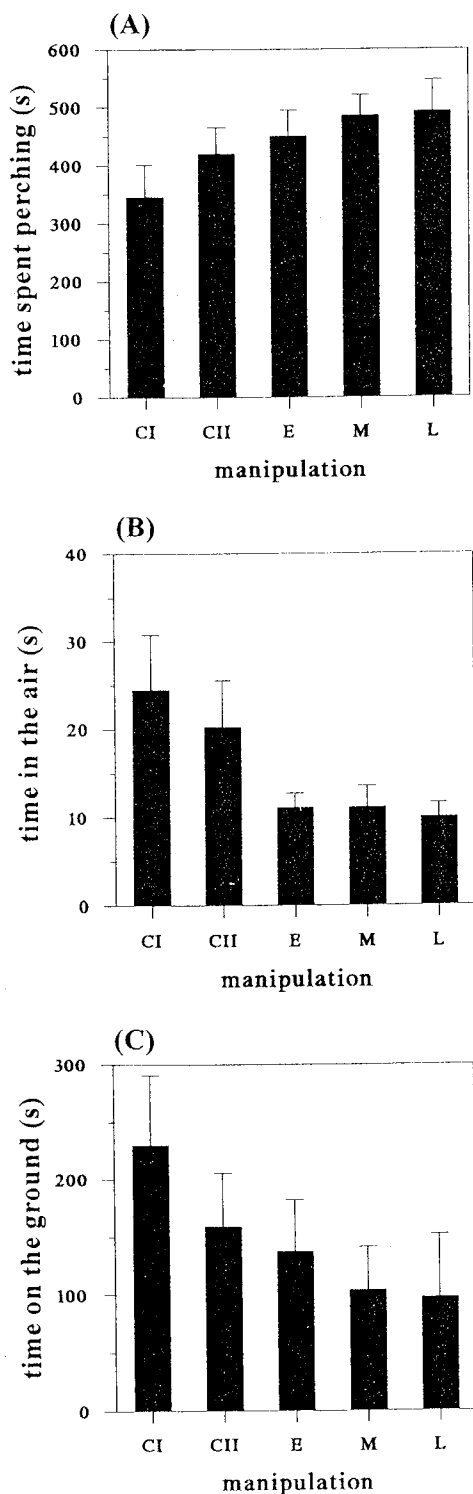
**Fig. 5.** Mean (+ SE) number of row contacts made in the aerial maneuverability testing course versus molt simulation group. Solid bars represent measures taken 1 week before, open bars measures taken immediately after, and hatched bars measures taken 2 weeks after the plumage manipulations. When data from before and immediately following the manipulations were compared, treatments differed significantly in terms of change in the number of row contacts ( $F_{[4,39]} = 2.62, P = 0.050$ ; orthogonal pairwise contrasts, control I and control II vs. early, mid, and late,  $P = 0.0066$ ; early vs. late,  $P = 0.886$ ; mid vs. early and late,  $P = 0.182$ ; control I vs. control II,  $P = 0.568$ ). When data from before and 2 weeks after the manipulations were compared, treatment groups did not differ significantly ( $F_{[4,39]} = 0.49, P = 0.742$ ).



**Fig. 6.** Mean (+ SE) level-flight speed versus molt-simulation group.



**Fig. 7.** Mean (+ SE) time (s) spent on perches (A), in the air (B), and on the ground (C) during the activity budget observations versus molt-treatment group. The manipulations significantly influenced time spent on perches ( $S = 14.40$ ,  $df = 4$ ,  $P = 0.006$ ; contrasts, early, mid, and late vs. control I and control II,  $P = 0.022$ ; early vs. mid vs. late,  $P = 0.181$ ; control I vs. control II,  $P = 0.151$ ) and in the air ( $S = 11.43$ ,  $df = 4$ ,  $P = 0.023$ ; contrasts, early, mid, and late vs. control I and control II,  $P = 0.022$ ; early vs. mid vs. late,  $P = 1.00$ ; control I vs. control II,  $P = 0.205$ ), but not on the ground ( $S = 9.03$ ,  $df = 4$ ,  $P = 0.061$ ).



less time on the ground, although the difference was not significant ( $S = 9.03$ ,  $df = 4$ ,  $P = 0.061$ ; Fig. 7C). The effects of the manipulations on the activity variables were less clear-cut. The manipulations significantly affected the time that the birds spent performing no activity (Fig. 8A), but none of the pairwise contrasts were significant (see Fig. 8). There was a nonsignificant tendency for the manipulated birds to spend less time feeding (Fig. 8B). However, there were no significant differences between treatment groups with respect to time spent in nonflying locomotion (Fig. 8C), vocalization (Fig. 8D), self-maintenance (Fig. 8E), or social interactions (Fig. 8F).

## Discussion

### Flight performance

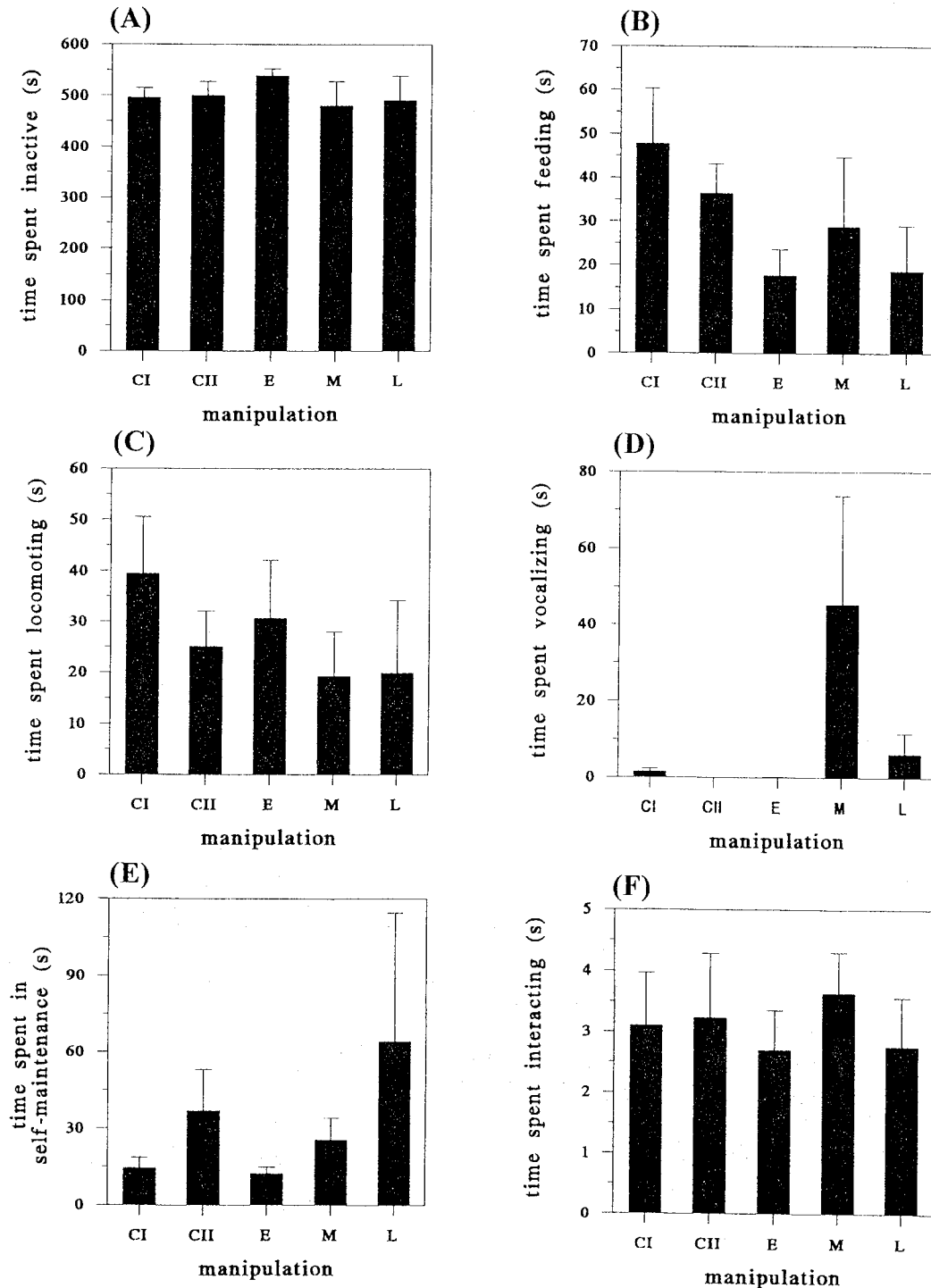
These results clearly indicate that primary and tail molt influence flight performance in the starling. During molt, birds show a reduction in level-flight speed, a decreased ability to take off from the ground, and a reduced capacity to negotiate an aerial maneuverability testing course. These impairments of flight are likely to be of general ecological importance and to directly affect individual survival. For example, the ability to take off quickly from the ground is likely to influence terrestrial predation risk (Lima 1993), and a reduction in aerial maneuverability is likely to increase the probability of being predated once airborne (see references in Witter et al. 1994).

Previously, only one laboratory-based study has attempted to quantify directly the relations between molt and aspects of flight performance. Tucker (1991) recorded the gliding performance of a single Harris' hawk, *Parabuteo unicinctus*, in a wind tunnel during natural molt stages (see also Tucker 1995). These observations revealed a U-shaped relation between flight cost (lift to drag ratio) and stage of primary feather molt: the bird incurred highest costs during mid-molt. Our study investigated changes in several aspects of flight performance both during natural molt and by experimental manipulations that simulated the wing geometries of different molt stages. In general accord with Tucker (1991), we found evidence for changes in flight performance over molt, and some of these changes were U-shaped. All flight parameters we recorded were significantly impaired over the whole of molt and there were some differences in flying ability between molt stages. Birds undergoing natural molt experienced a U-shaped change in angle of escape take-off throughout molt: it was steepest at the beginning and end of molt and lowest at mid-molt. In the experimental treatments, late-molt individuals flew faster during their escape-response take-off than early-molt birds. As only three experimental treatments were performed, it is possible that a U-shaped decrease in take-off speed may occur during simulated molt, but early molt was not an "early" enough stage to allow this relationship to be detected.

Our experimental manipulations represent a conservative test of the implications of molt for flight. First, we experimentally isolated the mechanical effects of feather loss and feather reduction from the physiological (and energy) costs of feather synthesis that would operate during natural molt. This approach was crucial to the experimental hypotheses we were testing, but is likely to underestimate the demands of



**Fig. 8.** Mean (+ SE) time (s) spent performing no observable activity (A), feeding (B), locomoting (C), vocalizing (D), self-maintenance (E), and interacting (F) during the activity-budget observations versus molt treatment group. The manipulations significantly affected the time that the birds spent performing no observable activity ( $S = 10.17$ ,  $df = 4$ ,  $P = 0.038$ ), but none of the contrasts were significant (control I and control II vs. early, mid, and late,  $P = 0.673$ ; early vs. mid vs. late,  $P = 0.277$ ; control I vs. control II,  $P = 0.554$ ). There were no significant effects on time spent feeding ( $S = 9.35$ ,  $df = 4$ ,  $P = 0.054$ ), locomoting ( $S = 3.75$ ,  $df = 4$ ,  $P = 0.441$ ), vocalizing ( $S = 4.20$ ,  $df = 4$ ,  $P = 0.381$ ), in self-maintenance ( $S = 0.91$ ,  $df = 4$ ,  $P = 0.922$ ), or interacting ( $S = 1.38$ ,  $df = 4$ ,  $P = 0.848$ ).



molt in the wild. Second, the manipulations we performed only affected the lengths of the primary and tail feathers and did not include manipulations of primary and tail asymmetry. Increased levels of asymmetry (fluctuating asymmetry; see

Ludwig 1932) are associated with primary feather regrowth in the starling (Swaddle and Witter 1994) and there is substantial evidence that primary and tail feather asymmetry reduce aerial maneuverability (Møller 1991; Evans et al.

1994; Swaddle et al. 1996) and other flight parameters (Thomas 1993). Levels of asymmetry are also known to vary with stage of primary growth (Swaddle and Witter 1994) and among traits and species (Møller and Höglund 1991; Balmford et al. 1993). Therefore, there may be different flight implications depending on the trait, species, and stage of growth, all of which require further examination.

The changes in flight performance between pre-molt and molt stages may not be as marked in the wild as reported in this experiment because pre-molt flight feathers *in vivo* may be damaged, abraded, or even missing (for a review see Jenni and Winkler 1994) and thus are likely to impair flight performance (Swaddle et al. 1996). Therefore, our experimental manipulations relate more closely to changes in flight ability between during-molt and post-molt stages of the annual cycle.

The apparent differences between the data obtained from the natural observations and the experimental treatments may reflect changes made by the birds (e.g., altering angle attack of wings, increasing amplitude of wingbeat) to compensate for the loss of sections of the wing. Birds in the experimental treatments were assessed immediately following the manipulations, and perhaps no time was allowed for any compensatory response. This contrasts with the birds in the experiment with natural plumage condition, which may have had time to adapt their take-off behavior to the change in their flight plumage. However, in natural molt the wing outline is constantly changing as feathers are shed and regrown; hence, there may be relatively little opportunity for birds to compensate fully for their change in wing geometry. Compensational changes were explicitly tested for in the experimental data. In terms of take-off speed and maneuverability, but not level-flight speed, manipulated birds were able to compensate for the experimental manipulation within 2 weeks of the treatments being performed. The observed changes in body mass in response to the manipulations may be one form of change to compensate for the reduction in wing area. These changes in mass, though, were not sufficient to return wing loading to premanipulation levels across all treatment groups. Furthermore, the changes in body mass cannot entirely explain the compensational response, as the between-group changes in flight performance revealed by the ANOVA models were robust to the inclusion/exclusion of body mass as a covariate.

### Body mass

Body mass of birds in the molt-simulation treatments was lowered in relation to that of controls. Previously, the physiological and energy demands of feather synthesis and the mass of new feathers and associated tissues have been invoked to explain body mass changes throughout molt (e.g., Chilgren 1977; Newton 1968; Lindström et al. 1993). Our manipulations have demonstrated that changes to the flight feathers alone, independently of physiological processes, can result in changes in body mass similar to that observed in starlings during natural molt. The power required for flight (i.e., the rate of work done) increases with body mass (Pennycuick 1975; Rayner 1990). In birds in the molt-simulation treatments, body mass may have been reduced as an adaptive response to lessen these costs in the face of the experimentally or naturally reduced wing area (or altered wing geometry). The observed decrease in mass may act, for example,

to lower the energy costs of flight (Pennycuick 1975; Rayner 1990) and decrease the minimum turning radius (Andersson and Norberg 1981), thus improving take-off performance, level-flight speed, and aerial maneuverability. Our data cannot rule out the possibility that the changes in mass are a "passive" reflection of, for example, changes in the energy cost of flight or changes in activity budgets associated with the manipulations. Importantly, however, the results do make clear that changes to the flight feathers alone can result in changes in body mass. This is consistent with the view that mass is strategically reduced to compensate for a reduction in wing area (cf. Freed 1981; Norberg 1981; see Witter and Cuthill 1993).

While body mass reduction may be beneficial in terms of improving flight performance, it may also be associated with costs, the most obvious being an increase in the probability of starvation (McNamara and Houston 1990; Witter and Cuthill 1993). Thus, we would expect a trade-off between the benefits and costs of such mass reduction (Witter et al. 1995). This may account for the fact that only a partial compensation in wing loading was observed in our experiment.

### Behavior

Observations of the experimental birds indicated that in simulated stages of molt, they altered several aspects of their behavior. Molt birds spent less time in flight and more time occupying perches. It has been suggested that birds in natural molt may avoid prolonged flights and seek areas of cover in order to conserve energy for feather synthesis and thermoregulatory control (Haukioja 1971a). It has also been suggested that the reduced flying ability of molting birds may force individuals into cover as an antipredatory response (Newton 1966). Our data indicate that the birds' behavior can alter purely in response to changes in the flight feathers. The apparent reclusiveness and lack of locomotory activity recorded in previous studies of bird behavior during molt (Eyster 1954; Newton 1966; Haukioja 1971a; Chilgren 1975), therefore, may not necessarily have been solely driven by the need to conserve energy for feather regeneration or thermoregulatory requirements. These behaviors may be accounted for by the reduction in flying ability in molting birds, which may be associated with an increase in perceived predation risk (cf. Witter et al. 1994) or an increase in the energy cost of flight. However, given that feather synthesis and thermoregulation during molt are energetically costly (Lustick 1970; Lindström et al. 1993), birds may exhibit these behavioral changes for both energy- and antipredation-related reasons.

### General

Starlings show decreased flight performance during natural molt. In previous studies, changes in flight performance have often been attributed to the decreases in the area of the wing and tail surfaces that occur during molt. Changes in flight performance and behavior have also been attributed to the energy-related and physiological processes that underlie avian molt, such as the decreases in flight muscle mass due to the protein demands of feather synthesis (e.g., Murphy and King 1992; Hohman 1993), the physiological costs of alterations in bone metabolism (e.g., Meister 1951; Murphy and King 1992), and increases in the basal metabolic rate (Lindström et al. 1993). By experimentally manipulating the

flight plumage to mimic stages of natural molt, we have been able to isolate the biomechanical consequences of feather molt independently of these inherent physiological changes. We have demonstrated that such changes in the flight feathers have important functional consequences. Birds in simulated molt have reduced take-off ability, impaired aerial maneuverability, and fly more slowly in level flight. The changes in flight performance that we observed are likely to directly influence aspects of individual survival (Hedenström 1992; Lima 1993; Witter et al. 1994; Swaddle et al. 1996). In association with the reduction in flight performance, molting birds reduce their body mass, fly less, and devote more time to energy-conserving activities. These findings have important implications for strategies of avian molt. It has been noted previously that although the physiological and energy costs of feather replacement are well characterized, they may not be sufficient to explain the separation of molt from other activities, such as reproduction, particularly in species that exhibit slow or partial molt (Murphy and King 1992). Consideration of the indirect functional consequences revealed by our study may be just as relevant in helping to explain the timing, duration, and pattern of molt as the more established physiological costs (cf. Earnst 1992).

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