

# Adaptive significance of avian beak morphology for ectoparasite control

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The beaks of Darwin's finches and other birds are among the best known examples of adaptive evolution. Beak morphology is usually interpreted in relation to its critical role in feeding. However, the beak also plays an important role in preening, which is the first line of defence against harmful ectoparasites such as feather lice, fleas, bugs, flies, ticks and feather mites. Here, we show a feature of the beak specifically adapted for ectoparasite control. Experimental trimming of the tiny (1–2 mm) maxillary overhang of rock pigeons (*Columba livia*) had no effect on feeding efficiency, yet triggered a dramatic increase in feather lice and the feather damage they cause. The overhang functions by generating a shearing force against the tip of the lower mandible, which moves forward remarkably quickly during preening, at up to 31 times per second. This force damages parasite exoskeletons, significantly enhancing the efficiency of preening for parasite control. Overhangs longer than the natural mean of 1.6 mm break significantly more often than short overhangs. Hence, stabilizing selection will favour overhangs of intermediate length. The adaptive radiation of beak morphology should be re-assessed with both feeding and preening in mind.

**Keywords:** coevolution; host; parasite; evolution; birds; lice

## 1. INTRODUCTION

Beak size and shape are often closely adapted to the particular food resources available in a bird's environment (Storer 1971; Grant 1986; Gosler 1987; Benkman & Lindholm 1991; Smith 1993; Gosler & Carruthers 1994; Weiner 1995; Barbosa & Moreno 1999; Bardwell *et al.* 2001; Grant & Grant 2002; Marquiss & Rae 2002; Parchman & Benkman 2002; Temeles & Kress 2003). However, other functions of the beak have been relatively ignored. Recent comparative work suggests that some features of beak morphology may be adapted to deal with other environmental challenges, such as harmful ectoparasites (Marshall 1981; Moyer *et al.* in press). For example, species of birds with long maxillary overhangs (figure 1a) have fewer feather lice than species with short overhangs (Clayton & Walther 2001). Similarly, within species, populations with long overhangs have fewer lice than populations with short overhangs (Moyer *et al.* 2002b). These correlations suggest that the overhang plays an important role in ectoparasite control by preening.

We tested the functional significance of the maxillary overhang using rock pigeons and their two common species of feather lice: *Columbicola columbae* and *Campanulotes compar* (Phthiraptera: Ischnocera). Both lice are permanent ectoparasites that spend their entire life cycle on the body of the host, where they feed on feathers and dead skin. They exert selection pressure on the host because the feather damage they cause reduces host mating success (Clayton 1990), thermoregulatory ability (Booth *et al.* 1993) and survival (Clayton *et al.* 1999).

To test whether the maxillary overhang enhances preening, we trimmed it from experimental birds

(figure 1a,b) and monitored their lice over time. The first of two such experiments involved wild-caught nestlings infested with lice from their parents (Clayton & Tompkins 1994). We chose nestlings to control for developmental plasticity, i.e. the possibility that birds growing up without an overhang might somehow compensate for its absence. Trimming nestlings also controlled for disruption to established sensory feedback mechanisms of adult birds. We further tested the role of the overhang with a 'rescue' experiment involving wild-caught adult pigeons with trimmed overhangs that were allowed to grow back. In addition, we documented the amount of feather damage caused by lice in the rescue experiment.

We also explored the role of the maxillary overhang in foraging. Trimming of the overhang had no effect on feeding efficiency, suggesting that it is a specific adaptation for ectoparasite control. Clayton & Walther (2001) hypothesized that the overhang enhances preening by generating a shearing force sufficient to damage lice, which are dorsoventrally flattened and have tough exoskeletons (Marshall 1981). Birds without overhangs could have difficulty killing lice and other ectoparasites because the vertical forces exerted between the tips of a straight maxilla and mandible are relatively weak (Bock 1966). The shearing hypothesis assumes that force is created by forward movement of the lower mandible, relative to the maxillary overhang.

We confirmed the shearing hypothesis using a combination of high-speed video observations and direct measurements of beak movements with electronic devices attached to the beak. To determine whether the forces generated are sufficient to damage lice, we compared the condition of lice preened by birds with and without overhangs. We also tested whether longer overhangs are more prone to breaking, which would constrain overhang length.

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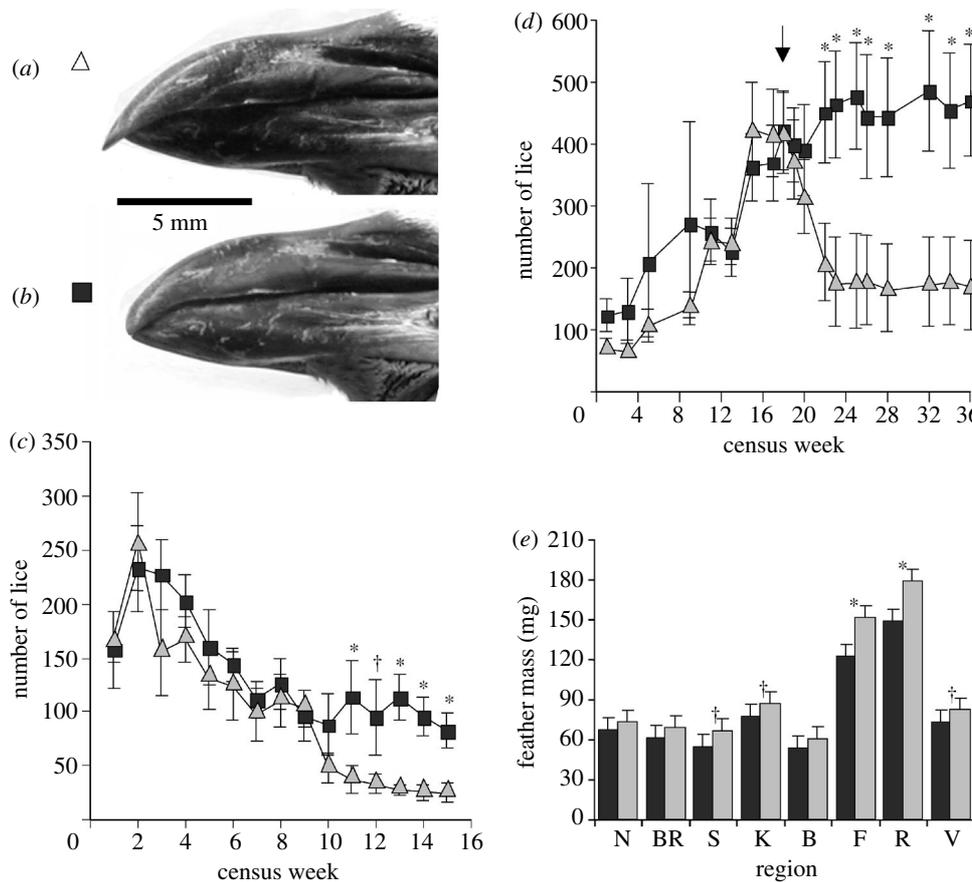


Figure 1. Impact of the maxillary overhang on feather lice. Rock pigeon beak before (a) and after (b) trimming of the overhang. (c) Mean ( $\pm 1$  s.e.) number of lice on young pigeons with trimmed (black squares) versus normal (grey triangles) overhangs ( $n=7$  per treatment). Data were analysed using a 2 (treatment: trim, control)  $\times$  15 (census) ANOVA with repeated measures on the second factor (census). There were significant overall effects of treatment ( $p=0.012$ ) and census ( $p<0.0001$ ), and a significant interaction ( $p=0.002$ ). The effect of treatment was clarified for each census using a protected  $t$ -procedure (Fisher's least significant difference test; Howell 1989). Trimmed birds had significantly more lice than controls for censuses 11–15 ( $t(168)>1.97$ ,  $*p<0.001$ ;  $\dagger p<0.05$ ). (d) Mean ( $\pm 1$  s.e.) number of lice on 26 adult pigeons in a rescue experiment. The overhangs of all birds were trimmed for 17 weeks; at week 18 (arrow), half the birds (grey triangles) were allowed to regrow their overhangs, while the remaining half (black squares) continued to be trimmed weekly. Data were analysed using a 2 (treatment: trim, regrow)  $\times$  11 (post-treatment census) ANOVA with repeated measures on the second factor (census). There were significant overall effects of treatment ( $p=0.003$ ) and census ( $p<0.0001$ ), and a significant interaction ( $p<0.0001$ ). Birds allowed to regrow their overhangs had significantly fewer lice than trimmed birds at each of the final eight censuses = weeks 22 to 36 (protected  $t(240)>1.97$ ,  $*p<0.001$ ). (e) Mean ( $\pm 1$  s.e.) feather mass of 13 birds trimmed throughout the rescue experiment (black bars), compared with 13 birds allowed to regrow their overhangs (grey bars). Feather regions sampled included the neck (N), breast (BR), side (S), keel (K), back (B), flank (F), rump (R) and vent (V). Data were analysed using a 2 (treatment: trim, regrow)  $\times$  8 (body regions) ANOVA with repeated measures on the second factor (region). There were significant overall effects of treatment ( $p=0.0002$ ) and region ( $p<0.0001$ ), and a significant interaction ( $p<0.0001$ ). Birds allowed to regrow their overhangs maintained significantly greater feather mass on their side, keel, flank, rump and vent regions (protected  $t(168)>1.97$ ,  $*p<0.001$ ;  $\dagger p<0.05$ ).

## 2. MATERIAL AND METHODS

### (a) Overhang trimming experiment: nestlings

The experiment involved 14 recently hatched birds still in their nests on rooftops in Salt Lake City, Utah. Birds with similar hatching dates were assigned to pairs, with one experimental and one control bird assigned at random. The overhangs of experimental birds were trimmed with the abrasive disk of a Craftsman rotary tool. Trimming is a minor procedure, analogous to trimming a fingernail; it removes no perfused tissue and draws no blood. The procedure was repeated weekly throughout the experiment to prevent overhang regrowth, which takes 2–4 weeks (unpublished data). Control birds were sham-trimmed at weekly intervals with a buffing disk.

All birds were manipulated first at 2 weeks of age, prior to developing the motor skills needed for preening. They were removed from the nest at 4 weeks of age and kept in

the laboratory for the duration of the experiment. The birds were maintained on a 12 h photoperiod in our animal facility at room temperature and 50% relative humidity. They were housed individually in wire mesh cages ( $30\times 30\times 56$  cm<sup>3</sup>) and provided *ad libitum* pigeon mix, grit and water.

Louse loads were censused weekly, starting when the birds were 6 weeks old, using the visual examination method of Clayton & Drown (2001), which accurately estimates the total number of *C. columbae* and *C. compar*. Louse load was calculated as the sum of the two species of lice.

### (b) Overhang rescue experiment: adults

Twenty-six adult birds were captured using walk-in traps baited with grain at several sites in Salt Lake City, Utah. The birds were housed as described for nestlings. The prevalence of lice on adult wild pigeons at this location was

only 47%. Therefore, we 'seeded' birds with lice using methods similar to those in Moyer *et al.* (2002a). Seeding had the desired effect; by the start of the experiment all birds were parasitized with approximately 100 lice each. Louse loads were censused at about 10-day intervals using the visual examination method of Clayton & Drown (2001).

During the first half of the 36-week experiment we trimmed the overhangs of all birds every week. Starting on the 18th week, we allowed the overhangs of half the birds, chosen at random, to grow back, while continuing to trim the remaining birds every week. We checked for side effects of trimming on host condition by monitoring body mass, which did not differ significantly even after 36 weeks. The mean ( $\pm 1$  s.e.) body masses of trimmed and regrown birds, respectively, were  $363 \pm 9.7$  and  $360 \pm 9.7$  g ( $t(24) = 0.20$ ,  $p = 0.85$ ).

We checked for side effects of trimming on preening effort by comparing the preening rates of trimmed and regrown birds on six occasions during weeks 18–36, using periodic bouts of scan sampling, as described in Clayton (1990). We tested for an effect of beak treatment on preening rate using a 2 (treatment: trim, regrow)  $\times$  8 (week) ANOVA with repeated measures on the second factor (week). Birds in the trim treatment spent a mean of  $13.6 \pm 0.9\%$  of their time preening, compared with  $14.5 \pm 1.2\%$  by birds in the regrow treatment. A repeated measures ANOVA on the preening data revealed a significant effect of week ( $F_{5,120} = 3.2$ ,  $p = 0.01$ ), but no effect of beak treatment ( $F_{1,24} = 0.30$ ,  $p = 0.59$ ), and no week  $\times$  treatment interaction ( $F_{5,120} = 1.9$ ,  $p = 0.10$ ). Beak treatment did not affect the amount of time birds spent preening.

We compared the extent of feather damage in trimmed versus regrown birds by weighing feather samples, as in previous studies (Clayton 1990; Booth *et al.* 1993; Clayton *et al.* 1999). We weighed the 10 longest feathers of a clump plucked from each of eight body regions (figure 1e). The feather samples were weighed to the nearest 0.01 mg on an analytical balance. We tested for an effect of beak treatment on feather mass using a 2 (treatment: trim, regrow)  $\times$  8 (body regions) ANOVA with repeated measures on the second factor (body regions).

### (c) Feeding experiment

We tested the role of the overhang in feeding by comparing the time it took birds to pick up seeds of different sizes before and after manipulating the bill in a repeated measures design. We used wild-caught birds acclimated to captivity for at least 5 months. Rock pigeons feed on a diversity of seed types; corn is the most important winter food and peas are preferred during summer months (Johnston & Janiga 1995). We tested birds using a range of seed sizes and shapes, including corn (mean length =  $8.5 \pm 0.26$  mm, width =  $5.9 \pm 0.12$  mm), peas (diameter =  $6.7 \pm 0.25$  mm) and milo (diameter =  $3.8 \pm 0.1$  mm). All birds were presented with the three seed types in a random sequence over a period of 3 days (one type per day).

Feeding trials were run with birds deprived of food for 20 h. Visual dividers were placed between cages to prevent any social influence on feeding. The animal room was darkened while setting up each trial, and a video surveillance system was used to monitor behaviour. Five seeds of a given type were arranged approximately 1 cm apart in a row across a Petri dish lined with soil, which approximated natural substrate. After placing the dish in the subject's cage and leaving the room, the lights were turned on, and the time

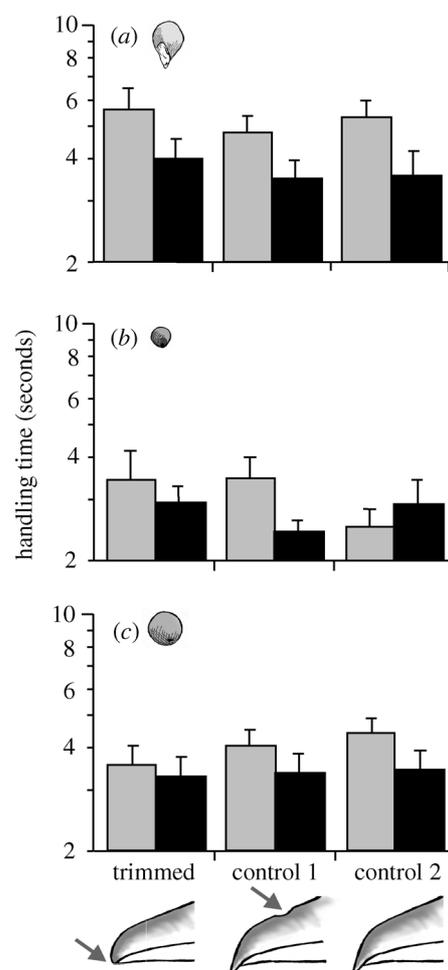


Figure 2. Mean ( $\pm 1$  s.e.) time for rock pigeons to consume five seeds of (a) corn, (b) milo, or (c) peas (drawn to same scale), before (grey bars) and after (black bars) one of the following treatments (number of birds): trim overhang ( $n = 13$ ), control 1 ( $n = 12$ ) and control 2 ( $n = 10$ ). Note log scale on y-axis. Control 1 birds had a narrow, 2 mm strip trimmed from the dorsal part of the maxilla (culmen) to simulate any stress that experimental birds may have experienced when their overhangs were trimmed (but without altering the beak surface used in feeding). Control 2 birds had their overhangs sham-trimmed with a buffing disk. The effect of treatment on handling time was tested using a 3 (treatment)  $\times$  3 (seed type)  $\times$  2 (trial: before or after treatment) ANOVA with repeated measures on the second and third factors (seed type and trial). Handling time data were normalized prior to analysis using log transformations. There were significant main effects of seed type ( $p < 0.0001$ ) and trial ( $p = 0.0001$ ) on handling time, but no effect of bill treatment on handling time ( $p = 0.88$ ), nor any significant two- or three-way interactions between bill treatment, seed type and trial ( $p > 0.10$ ).

between the bird picking up the first and last seeds was measured to the nearest 0.1 s. If a bird paused for more than 3 s between seeds, the timer was stopped until the bird resumed feeding. At the conclusion of each trial, birds were allowed to feed *ad libitum* for several hours.

The day following the third trial we randomly assigned birds to one of three treatments: experimental (overhang trimmed), control 1 or control 2 (see figure 2). Following treatment, feeding trials were repeated in a random sequence with one seed type per day, as before. We used a repeated measures design to compare the change in handling time for

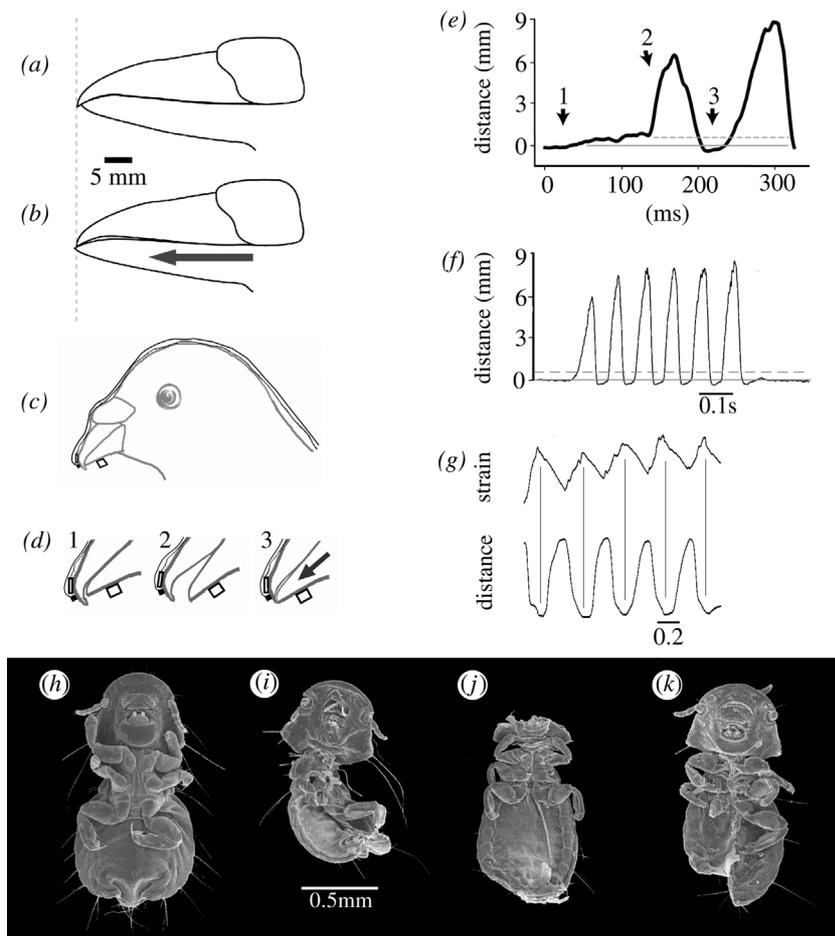


Figure 3. Beak tracings from high-speed video of a rock pigeon preening a neck feather (not shown) before (a) and after (b) forward movement of the lower mandible. (c) Experimental set-up for recording beak movements during preening. A magneto-sensitive transducer is glued near the tip of the maxilla and a rare-earth magnet is glued to the lower mandible, set back 5 mm relative to the transducer. The offset placement of the transducer and magnet ensures that forward movement of the lower mandible can be detected as a voltage decreasing below the value of the closed beak (see below). A small strain gauge (black square) is also glued to the tip of the maxilla in front of the transducer. (d) Diagram of beak movements when preening, in relation to (e) voltage output of the transducer. Before preening the beak is closed in the resting position (d1), with voltage calibrated at zero (e1; solid grey line). As the bird takes a feather into its beak and positions it, the voltage increases to about 1 mm (dashed grey line). When preening starts, the bird opens its beak (d2) to a reading of several millimetres (e2), then closes it and moves the lower mandible forward (d3), thus dropping the voltage below the zero line (e3). The amount of forward movement is the distance between the lowest reading and the dashed grey line. (f) Typical bout of preening showing rapid cyclical forward movement of the lower mandible. (g) Uncalibrated voltage output from the strain gauge (strain), with simultaneous recordings from the transducer (distance). Note that increases in strain accompany forward movements of the lower mandible. The positive overall slope is an artefact of a slight temperature increase in the strain gauge, which was not temperature compensated. The temporal pattern and amplitude of the beak movements on different feathers varies somewhat. (h) s.e.m. of an undamaged louse (*Campanulotes compar*), compared with lice that have had most of their legs removed (i), or been decapitated (j), or lacerated (k) by birds with normal overhangs.

each of three seed types before and after treatment. Birds were excluded from the analysis if they had unsuccessful trials owing to technical difficulties, such as stepping on the food dish and overturning it.

#### (d) *Beak movements: high-speed video*

We video taped preening by three wild-caught birds at a rate of 250 Hz using an NEC high-speed video camera with a macro zoom lens (Nikor 55 mm 1–2.8f). Birds were isolated in cages (30 × 30 × 56 cm<sup>3</sup>) under non-heat producing 120 W halogen lights. We did a frame-by-frame analysis of the movement of the lower mandible in relation to the maxillary overhang. The tip of the beak (approximately 1 mm) was often hidden from view within the feather being preened. We therefore used the fleshy white cere at the base of the maxilla

as an optical marker to determine the relative positions of the overhang and lower mandibular tip throughout the preening sequence (see video at <http://darwin.biology.utah.edu/preen.html>).

#### (e) *Beak movements: electronic recording of beak movements*

Six wild-caught birds were used for electronic recordings. Each bird was fitted with an elastic belt around its thorax. The belt contained a Velcro tab on the back for attachment of wire connections in a small backpack. Birds were tethered with another wire leading from the backpack to a balance tether arm, adjusted using a counterweight. The apparatus relieved each bird of the added weight of its backpack, while allowing it to move freely about the cage without getting tangled in

the wires. Each bird was also fitted with an Elizabethan collar that prevented it from preening. Birds preened readily upon removal of the collar at the start of the recording session.

Once birds were accustomed to their tethers and collars (after 1–2 days), we used cyanoacrylate to glue a magneto-sensitive transducer to the upper maxilla and a rare-earth magnet to the lower mandible (figure 3*c,d*). After the glue set, wires from the transducer were routed over the head to a Velcro tab on the bird's back, where a connection to stronger wire was made. The signal from the transducer was amplified (100×; Brownlee 410) and recorded on a multi channel data recorder (TEAC 135T), along with a voice channel to record comments by the observer. For each bird we recorded all preening bouts taking place over a period of 2–4 h. Recordings were played back, digitized (Data Translation 2821G; 10 kHz bandwidth), stored and analysed using SIGNAL 3.1 software (Engineering Design).

We calibrated the magnetic transducer *in situ* for two birds by inserting cardboard pieces of known width between the tips of the upper maxilla and lower mandible, then recording the voltage output of the system. For calibration of the forward movement of the lower bill we manually brought the tip of the lower bill forward to meet the tip of the maxilla and recorded the voltage output. We also verified that small sideways movement of the mandibles did not cause voltage fluctuations of the magnitude observed in the recordings during preening.

In two birds we used a small strain gauge to record compressive strain on the beak during preening (figure 3*c,d*). The strain gauge (Entran ESB-020-500) was custom made in a half-bridge design and encased in epoxy resin. The voltage output of the strain transducer was amplified (Brownlee 410) and simultaneously recorded on another channel of the recorder.

#### (f) *Damage to lice*

We tested the impact of the bill overhang on louse morphology by examining lice collected beneath the cages of birds with and without overhangs. First, we blocked the preening ability of six wild-caught pigeons by fitting them with Elizabethan collars. Each bird was seeded with lice and housed individually for several months to allow their louse populations to increase. The lice were counted using the visual examination method (Clayton & Drown 2001) and birds were matched into three pairs based on similar louse loads. The overhang of one randomly chosen bird in each pair was trimmed and the other bird was sham-trimmed. Birds were then transferred to modified cages surrounded by sheets of Plexiglass and paper, which allowed passage of air and light, while ensuring that lice removed by preening fell directly into a tray beneath the cage. The collars were removed from all birds to restore their preening ability, and lice accumulating in the trays were collected 48 and 96 h later. A randomly chosen sample of 100 lice from each tray was examined blind to host treatment (40× magnification) and scored as normal or damaged (crushed, decapitated, lacerated and/or missing greater than or equal to three legs).

#### (g) *Overhang breakage*

To investigate the relationship between overhang length and risk of breakage, we captured 124 wild pigeons and allowed them to acclimate to captivity for at least 1 month. The beaks of all birds were in good condition with no deformities, chips or fractures. We measured the length of the overhang for each

bird to the nearest 0.05 mm using calipers. Overhang length was the straight-line distance from the tip of the maxilla to the point at which it intersects the tip of the lower mandible. Each bird was measured three times, and the mean value calculated. Repeatability of this measurement was high ( $r > 0.97$ ; Lessells & Boag 1987). We added a piece of cuttlebone and a ceramic tile to each cage to provide abrasive surfaces similar to those birds encounter in the wild. We examined the condition of each bird's beak weekly, noting any chips or fractures, over a period of 1 month. At the end of this period we compared the initial length of broken overhangs to the initial length of intact overhangs.

### 3. RESULTS

#### (a) *Overhang trimming experiment: nestlings*

Birds with intact overhangs were much better at controlling their lice than birds without overhangs. Nestlings reduced their louse loads by more than half as they learned to preen, regardless of treatment. However, nestlings with trimmed overhangs had a mean of about 25 lice at the end of the experiment, compared with 100 lice on birds without overhangs (figure 1*c*).

#### (b) *Overhang rescue experiment: adults*

Trimming of the overhang triggered a fourfold increase in lice that levelled off at 15 weeks (figure 1*d*). Regrowth of the overhang, commencing at 18 weeks, caused an immediate reduction in lice that levelled off after 1 month (figure 1*d*). Birds trimmed throughout the study had significantly more feather damage (lower feather mass) than those allowed to regrow their overhangs (figure 1*e*). The difference in feather damage is striking considering that, throughout the first half of the experiment, the two groups of birds had similar louse loads and presumably comparable initial feather damage.

#### (c) *Feeding experiment*

Before treatment, birds averaged up to 5.5 s to pick up five seeds of a given type (figure 2*a–c*). Following treatment, birds increased their speed with experience for all three seed types, averaging less than 4.0 s to pick up five seeds of a given type. This improvement, and the fact that seed type had a significant effect on feeding efficiency (figure 2), indicates that the assay we used was sufficiently sensitive to detect subtle changes in feeding efficiency. Nevertheless, removal of the overhang had no significant impact on feeding efficiency (figure 2).

#### (d) *Beak movements*

The high-speed video revealed forward movement of the lower mandible in relation to the upper maxilla (figure 3*a,b* and video at <http://darwin.biology.utah.edu/preen.html>). The frequency of this movement was remarkably fast, at up to 31 times per second! Data from the magnetic transducer confirmed that the overhang and lower mandible work in concert at high frequency (figure 3*f*). Data from the strain gauge revealed that each forward movement of the mandible exerts compressive strain against the maxillary overhang (figure 3*g*). Peaks in strain coincided with the most forward position of the mandible or were immediately before or after the most forward position (not shown). This variable synchronization of forward movement and strain indicates that the edges

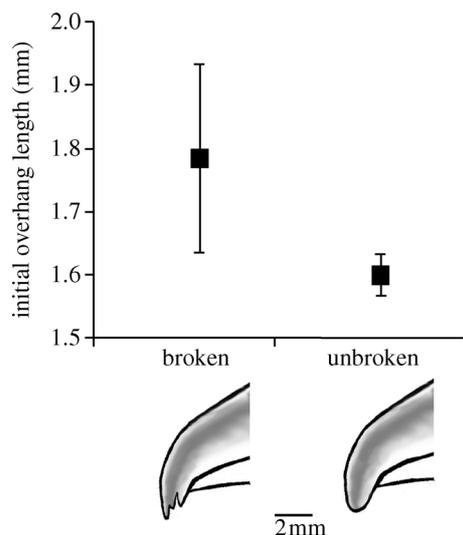


Figure 4. Relationship of overhang length to breakage. The overhangs of 13 birds that suffered breaks were initially longer than those of 111 birds without breaks; mean ( $\pm 1$  s.e.) =  $1.78 \pm 0.15$  mm versus  $1.60 \pm 0.03$  mm; Mann-Whitney test,  $Z = 2.01$ ,  $p < 0.05$ .

and tips of the overhang and lower mandible move past one another slightly, generating shearing forces.

#### (e) *Damage to lice*

Birds with normal overhangs removed significantly more lice than paired controls with trimmed overhangs ( $G \geq 22.2$ ,  $p < 0.0001$ ). Moreover, lice from birds with overhangs showed significantly more physical damage (figure 3*h-k*) than lice from birds without overhangs (replicated goodness of fit; Sokal & Rohlf 1981:  $G_{\text{Total}} = 13.7$ ,  $p < 0.01$ ;  $G_{\text{Pooled}} = 9.9$ ,  $p < 0.005$ ;  $G_{\text{Heterogeneity}} = 3.8$ ,  $p > 0.1$ ). Much of this damage was consistent with shearing forces, e.g. missing legs (figure 3*i*), decapitation (figure 3*j*) and lacerations of the tough exoskeleton (figure 3*k*).

#### (f) *Overhang breakage*

Over the course of 1 month, 13 of 124 birds (10.5%) broke their overhangs, with damage ranging from ragged chips to fissures extending several millimetres into the maxilla. Birds with broken overhangs had significantly longer overhangs at the start of the month than did birds whose overhangs remained intact (figure 4).

## 4. DISCUSSION

Our results show that the maxillary overhang enhances preening for ectoparasite control. Efficient preening prevents increases in lice and the feather damage they cause. The highest louse loads we observed, and their associated feather damage, were within the range of natural variation documented in earlier field studies (Booth *et al.* 1993; Clayton *et al.* 1999). Louse loads of this size lower host fitness by reducing host mating success (Clayton 1990), thermoregulatory ability (Booth *et al.* 1993) and survival (Clayton *et al.* 1999). Thus, lice are expected to select for efficient host defences, such as the maxillary overhang.

In order to damage lice, the maxillary overhang must be long enough to serve as a template against which the tip of

the lower mandible can generate force. However, overhangs that are too long could incur a cost. For example, long overhangs might impair feeding ability. Because removal of the overhang had no significant effect on feeding efficiency (figure 2), it seems unlikely that its current length is constrained by trophic selection. Another possible constraint is that long overhangs are more prone to break than short ones, as demonstrated by our results. Broken overhangs have severe consequences for wild birds; rock pigeons with broken overhangs have thousands of lice and extensive feather damage (Clayton *et al.* 1999). Hence, overhangs of intermediate length are the expected compromise between selection for ectoparasite removal favouring longer overhangs, and counter selection arising when overhangs are too long and get broken.

The adaptive radiation of beak morphology should be re-assessed with both feeding and preening in mind. Although the role of preening in controlling ectoparasites has long been recognized (Rothschild & Clay 1952; Brown 1972), this is the first study to demonstrate a specific adaptation that enhances preening efficiency. More research is needed to determine exactly how the overhang functions; e.g. is the relationship between overhang length and preening efficiency linear or a threshold effect? Additional work is also needed to determine the role of the overhang in other species of birds. Although the overhang does not impair feeding in rock pigeons, this is not likely to be true for all birds. Woodpeckers, scythebills, hummingbirds, herons, darters, skimmers and oystercatchers have all lost the overhang (Moyer *et al.* in press), presumably because it hinders modes of foraging such as pounding or probing wood, sipping nectar, prying open bivalves and spearing or skimming up fishes. These taxa, all of which have lice (Price *et al.* 2003) and other ectoparasites, presumably depend on other defences, such as scratching, sunning, feather chemistry and immune responses (Clayton & Moore 1997; Moyer *et al.* in press).

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