Eyelid squinting during food-pecking in pigeons

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Significance statement: Pecking pigeons are a familiar sight. Ostheim et al. wondered why they close their eyes when their beak-tip approaches a seed and found they actually improve their vision by squinting.

Abstract

The visual control of pecking by pigeons (*Columba livia*) has latterly been thought to be restricted to the fixation stops interrupting their downward head movements because these stops prevent interference by motion blur. Pigeons were also assumed to close their eyes during the final head thrust of the peck. Here we re-examine their pecking motions using high-speed video recordings and supplementary provisions that permitted a three-dimensional spatial analysis of the movement, including measurements of their pupil diameters and eyelid slit width. The results confirm that pigeons do not close their eyes completely during the presumed optically ballistic phase of pecking. Instead their eyelids are narrowed to a slit. The width of this slit is sensitive to both the ambient illumination levels and the visual backgrounds against which seed targets have to be detected and grasped. There is also evidence of some interaction between pupil diameter and eyelid slit width. We surmise that besides being an eye-protecting reflex, the partial covering of the pupil with the eyelids may increase the depth of focus, enabling pigeons to obtain sharp retinal images of peck target items at very close range and during the beak-gape 'handling' of food items and occasional grit particles.

Introduction

The pecking behaviour of birds and particularly that of pigeons has attracted considerable experimental interest in the past. Even setting aside the extensive literature on conditioned key-pecking, there is also substantial information on spontaneous forage pecking. Although the complexity of the pecking motions was recognised at an early stage (Thorpe, 1951), pecking was nevertheless first classified as a fixed action pattern (Tinbergen, 1951). More modern research led to a partial re-evaluation of this characterisation by allowing for the existence of some motion plasticity (e.g., Schleidt, 1974; Barlow, 1977; Pellis, 1985) but stereotypy continued to be stressed in connection with at least some phases of pecking (Zeigler et al., 1980; Zweers, 1982; Goodale, 1983). Later studies have however revealed that pecking is a remarkably flexible action pattern (Hörster, 1997). Even under invariant conditions, the pecking motions of a single pigeon can be surprisingly variable (Siemann and Delius, 1992). Several authors have reported that the final down-thrust of the pigeon's head is preceded by a series of saccade-like head movements punctuated by fixation arrests. During the last two fixation stops, F1 and F2, the head is held above the target item, moves closer, but at F1 the beak tip still remains well away from the target. The gap between eye and target is relatively constant (50 to 70 mm) during the last fixation pause (F2), varying only slightly depending on the size of the targets (Klein et al., 1985). Theunissen and colleagues (2017) more recently reported that when pigeons pecked at visual stimuli displayed on a vertical computer screen furnished with an infrared touch screen for food reward, the first and second fixations were interactively concerned with taking aim at stimuli of between 5 and 32 mm diameter and that an additional colour discrimination did not detectably alter this circumstance. These authors however tended to discount an optical role for the eyelid slit formation that they also observed.

The final down-thrust begins when the head descends from the F2 pause towards the target. From that stop, it takes approximately 60 ms until the seed is grasped. It is during this final motion phase that the eyes gradually close (Hodos et al., 1976; Zeigler et al., 1980). Delius (1985) proposed that the eyelid closure or blink was a protective reflex against the backscatter of particles raised by the impact of the beak-tip on the substrate. Since the eyes were supposed to be closed during a major part of the final down-thrust, a visual steering of its course seemed unlikely. The terminal phase of pecks was thus termed a ballistic (feed-forward, open-loop) movement that was only controlled by visual information collected during F2 (Zeigler et al., 1980; Wohlschläger et al., 1993). Based upon these arguments, Zweers and colleagues (1994) regarded pecking as a sequence of alternating static and dynamic phases in which exteroceptive

information that controls the motor patterning in a subsequent dynamic phase is gathered only within each preceding static fixation phase.

However, higher frequency recordings occasionally reveal final approach trajectories that cannot be easily accounted for on the basis of F2-originated information alone. Siemann and Delius (1992, their Fig. 3), for example, showed head acceleration data that implied that the final descending phase varied substantially across individual pecks. The same is suggested by head velocity data derived from high-speed cinematography (Klein et al., 1985). High-speed video recordings also revealed that, on occasion, already initiated approach movements can still be either corrected or arrested in mid-course. A figure shown by Ostheim (1994), for example, showed a peck that was abruptly stopped when the bill tip was only about 5 mm above the ground and remained there for some 0.5 s before the target, a millet seed, was finally grasped. Since the bill did not touch a seed or the ground before the grasping, eyelid slit mediated visual information seems to have intervened.

That at least some visual input steers the final peck down-thrust was also suggested by the fact that convergent eye movements maintaining binocular optical fusion accompany this phase. Maximal ocular convergence pertains just before the bill contacts the substrate (Martinoya et al., 1984; Jäger et al., 1987; Nalbach et al., 1993; Wohlschläger et al., 1993), just when the eyes were assumed to be closed. A more careful inspection of published cinematographic sequences, however, reveals that the eyes of pigeons are in fact never completely closed during the course of a peck (e.g., Zeigler et al., 1980, their Fig. 1; cf. Yorzinski, 2016). An eyelid slit would allow at least some visual input to impinge on the retina while possibly functioning as a luminance controlling aperture co-acting with that of the pigeons' pupil (Campbell and Gregory, 1960; Marshall et al., 1973; Woodhouse and Campbell, 1975; Donovan, 1978; Miller, 1979; Levy and Sivak, 1980; Martin, 1983). If, on the other hand, the eyelid closure had a protective function against backscattered particles (Delius, 1985; see also Spring, 1965), then it should exhibit responsiveness to small grit particles added to the targeted seeds. Accounts of earlier preliminary research on this issue were already published by Ostheim (1997a, 1997b).

Material and Methods

Experiment I. Peck motions

This experiment was designed to determine more precisely than hitherto the kinematics of the eyelid slit narrowing and subsequent widening in relation to the pecking head movements occurring when pigeons feed on a seed out of a heap of seeds.

Subjects. Five adult domestic pigeons (*Columba livia*) of local homing bred from homing stock by the Animal Facility of the Universität Konstanz served as subjects. They were kept in individual $40 \times 45 \times 35$ cm wire grid cages located in a well-ventilated and illuminated (12 h on/12 h off) room. The pigeons' food was removed a day prior to a recording session. Each pigeon was exposed to a total of five sessions on as many consecutive days. All the experimental treatments described in this paper complied with the German animal welfare laws and regulations and were approved by the Tierschutzkomission Freiburg.

Procedure. Before a recording session began, an 8 mm diameter white sticky marker was affixed immediately ventro-posteriorly of the pigeon's left eye: it provided a convenient calibration base for adjusting image magnifications and for a computerized compensation of distortions due to oblique head positions with reference to the camera. The bird was then placed into a narrow elongated transparent acrylic chamber (70 x 10 x 25 cm) chamber with a 5 cm diameter glass dish on the floor at its left end. The pigeon was thus constrained to move its head within the focused field of a video camera (Sony Handycam) placed 50 cm away from the pigeon's left eye and at about the same height. The white-floored chamber stood on a white table within a white painted cubicle; this ensured an even and diffuse illumination. A stroboscope (Hornel Movystrop 350) set at 125 flashes/sec directed at the white ceiling yielded an average ambient luminance of 300 lx as measured with a photocell lux-meter (Mavolux Gossen) at the position of the pigeon's left eye. The high frequency of the flickering light amply exceeded the fusion threshold of pigeons (Delius et al., 2017).

Recording. 25 ml millet seed was dropped into the feeding bowl and video-recording began as soon as the pigeons started feeding. The camera fed into a videorecorder (Panasonic AG-7350 SVHS) that was also linked to a personal computer through a serial interface (Panasonic AG-IA232TC) to steer the video recording. Subsequently it also permitted separate access to video half-frames, thus providing a basic 50 frames/s resolution as the stroboscope produced 125 1-ms flashes/s and the camera was open-shutter operated. Each half-frame depicted two or three

superposed successive images but the computer was equipped with a frame grabber (Data Translation DT2853) and a program that ensured a clear viewing of the single images.

Measurements. The videotapes were reviewed on a nearly flat television monitor (36-inch Sony Super Trinitron); on it the pigeons' head sides appeared magnified about 6-fold. Six serial pecks per pigeon were selected from their third or fourth recording session, i.e., when they were well acquainted with the procedures. For each of the pecks, we identified the earliest half-video frame showing the seed actually being grasped with the bill. Then we sought out the 20 successive images preceding this event and the 20 successive images following it, thus covering an interval of 320 ms. The position of the posterior corner of the eyelids was marked with a mouse-driven cursor in all of these images. A specially written program enabled us to locate these marks and the target seed within a millimetric gridded xyz space, scaled according to the 8 mm white face marker worn by the pigeons. From this we then derived the distances between the eye centre and the target seed (henceforth eye-to-seed distance) with an estimated ±1.5 mm precision for each of the 40 images. The greatest width of the eyelid slit that regularly occurred towards its frontal end (see Figure 2B below) was measured with a calliper and converted into actual mm with ± 0.1 mm precision.

Experiment II. Eyelid aperture dynamics

Here we examined to which extent the width of the eyelid slit during serial pecks would be affected by both the ambient luminance and by grit intermixed with the target seeds. As the narrowest eyelid slit widths occurred at the moment of seed grasping in Experiment I, the slits were measured at this point of time in Experiment II. Whenever possible, we also measured the pupil diameters at the same point of time. As we did not observe systematic differences between these measurements and those of the preceding fixation head stop and the slit naturally obscured the outline of the pupil, we also took the pupil measurements at these points.

Subjects. The same five pigeons as in Experiment I were employed.

Procedure. The same basic set-up and general procedures as in Experiment I were used. However, besides the 25 ml *seed-only condition* we also tested a *grit-seed condition* in which 50 ml of a grit-grain mixture was poured into the feeding bowl. We also changed the *lighting conditions* in the chamber as to yield 1, 9, 20, 60, 100, 200, 300, 5000, and 20000 lx luminances. The 1 lx condition (equivalent to full-moon lighting) was obtained using four frosted filament

light bulbs (Osram 15 W) and the 9, 20, 60, 100, 200 and 300 lx luminance levels were generated with four fluorescent light bulbs (Osram Dulux EL, 15 W) directed at the room ceiling. At the standard voltage (220 V) the spectral composition of the light emitted by these bulbs was daylight-like; but the various voltages used to produce the different luminance levels somewhat modified their spectral composition. As the 9 and 20 lx conditions could be produced with either the filament bulbs or the fluorescent lamp, we were able to check that associated spectral differences had no detectable influence on the measures. To ensure stability, the bulbs were operated for 30 min before all recording sessions. For recordings at 5000 lx and 20000 lx, the chamber, decked with a glass pane, was placed on an outdoor table, either in the shade or in the sunshine at close to midday. The 5000 lx luminance could also be produced with fluorescent bulbs so that we could again check that the spectral differences had no pronounced effects. The various luminances were measured with the same lux-meter used in Experiment I. Note that the lux unit is geared to the spectral sensitivity of humans, that of pigeons differing somewhat (Blough, 1957; Remy and Emmerton, 1989), but we are reasonably certain that our response measurements were not appreciably affected by this circumstance. The pigeons were exposed to the two seed-alone and grit-seed by nine different luminance conditions in a quasi-random order; in all 18 sessions they were routinely allowed to adapt to the relevant lighting condition for 30 min before recording began.

Recording. With the higher luminances, we used the earlier employed Sony Handycam camera; in the 1 lx condition we employed a highly sensitive Panasonic-CCTV camera.

Measurements. The lighting now being continuous, each video half-frame only contained a single image, and the temporal resolution of the recordings was thus limited to 50 images/s. For a series of serial pecks, we selected (1) a half-frame belonging to the fixation stop preceding the seed approach movement to measure the pupil opening and (2) the half-frame corresponding to the instant when the seed was grasped to measure the eyelid slit width. Much as described earlier, the pupil diameter and the slit width was measured with a calliper and converted to mm. When the pupil's shape was oval – as it appeared to be when it was not quite orthogonally oriented to the camera's optical axis – we measured its longer axis. Note also that the pupil was subject to magnification because the cornea itself acted as a lens (Schaeffel and Howland, 1987). Alexandridis (1967) judged that in pigeons this magnification varied between 1.1 and 1.2× depending on the momentary accommodation state of the eye, doubtlessly reflecting the ongoing activity of Crampton's muscle. Since we measured the pupil at the moment of target-

seed fixation (F2), the accommodation state could be expected to be much the same across pecks and pigeons. As long as the pupil opening was not encroached by the eyelids, the aperture was given by its surface area $\pi \times r^2$; when the pupil was nearly symmetrically encroached by the eyelids, the remaining aperture was defined by a nearly rectangular $2r \times w$ (pupil diameter $\times$ slit width) area; however only when the eyelid slit width was markedly narrower than the pupil opening and when the slit was approximately 'centred' over the pupil. Otherwise the aperture was circle-segment shaped, its area being approximated by $2/3cw + w^3/2c$, where c and w are the dimensions of the segment's chord and width; or circle-strip shaped, where its area is that of the pupil minus that of the two segments covered by the two palpebra. Note that the pupil might have expanded under the narrowing eyelids to compensate for the retinal darkening this caused, an issue to which we return below.

At the instant of seed grasping, the eye-to-seed distance was equal to each pigeon's non-varying distance between its pupil centre and its bill tip, so that this measure only needed to be taken once for each bird. At the instant in which the pupil diameter was measured, the F2, the eye-to-seed distance, as explained above, could vary somewhat from peck to peck. To measure it for a given peck, a digitised version of the relevant video half-frame was displayed on the monitor screen. The centre of the pupil was marked with the aid of a mouse-driven cursor. Then we proceeded to the half-frame on which the eyelid slit was measured and similarly marked the bill-tip held seed on this second digitised image. The distance between the pupil centre and seed marks was computed and converted according to the same procedure described earlier for the eye-to-seed distance with an estimated precision of $\pm$ 0.5 mm. The reliability of these procedures was verified by having several different observers carry out the procedure on identical pecks and comparing. The 2 conditions $\times$ 9 luminances $\times$ 5 pigeons $\times$ 20 pecks yielded a total of 1800 measurement sets (slit width, pupil diameter, and eye-to-seed distance). These data were submitted to analyses of variance (GLMP procedure, SAS software).

III. High-speed images

After Experiments I and II were completed, an extremely high-speed video recording system became available. This made it possible to examine the millet-seed pecking of pigeons with a higher temporal resolution than before. Besides employing the standard lateral viewpoint, we also used an upward viewing perspective by recording through a glass floor, which yielded informative additional data.

The same five pigeons participated as before. A video camera (Weinberger System, Switzerland) operating at 500 frames/s (2 ms per frame) was utilized. Light from fluorescent bulbs illuminated each pigeon's head from a lateral-left position, providing a luminance of 1000 lx at its left eye but only 100 lx at its right eye. For one series of recordings, the floor of the experimental chamber was replaced by an optical quality glass plate. No feeding bowl was employed and only a few millet seeds at a time were sparsely offered directly strewn on this plate through a plastic pipe. The camera was placed below, pointing upwards through the plate so that its optical axis was approximately in line with the bill axis of the pigeons. For another series of recordings, the camera was located laterally at the pigeon's eye level, much as in Experiment II.

Results

Experiment I. Peck motions

The pigeons pecked in bouts, each consisting of some 50 to 200 serial pecks, most at the rate of approximately 3/s, until the seeds offered were consumed, this taking some 6–10 minutes altogether (by the way, not all pecks led to a seed ingestion). The bouts were interrupted by pauses lasting for a few to several tens of seconds, often with the head raised in an elevated vigilant attitude. Within the serial pecking bouts, the head rose to no more than 60 mm above the dish floor, a position that was held for a fraction of a second between pecks (i.e., fixation stops). We disregarded the first peck of any given bout and only analysed the subsequent, serial pecks within the bouts. The head only returned to F1 between blocks of serial pecks. All pecks we looked at in video slow motion (several hundred more than those evaluated here) evinced an only partial eyelid closure through which the eyeball surface could be discerned, and never a complete closure.

Figures 1A and B show the eye-to-seed distances and the slit widths during the 30 pecks analysed (6 pecks per 5 pigeons) plotted against time, all peck courses being synchronised with respect to the video image in which the seed was grasped with the bill. It can be appreciated that the head's approach movements begin about 80 ms before the seed grasping. Around this grasping, the head remained spatially nearly immobile for about 20 ms. The head elevation movement that followed lasted about 100 ms and was regularly accompanied by mandible and tongue motions subserving the swallowing of the seed. Before and after approach and withdrawal, the head remained at a nearly steady distance from the bowl floor. These longer stationary phases correspond to the more variable but on average about 300 ms long F2 fixation arrests during which the pigeons sought out the next target.

Although the trajectories of the different pecks varied somewhat, the individual pigeons produced reasonably uniform peck courses (Figure 1A). The differences between the pigeons arose mainly because they each had bills of slightly different lengths and furthermore each individual tended to start its pecks from somewhat differing fixating locations. Note that even the individual pigeons were not very precise about returning to the same initial fixation F2 locus after pecks. The vertical components of the peck trajectories were relatively large in amplitude but varied little between pecks. In contrast, both the horizontal (sidewards and anterior-posterior) movement components were of smaller amplitude but quite variable. The eye-to-seed distance courses in Figure 1A therefore mainly reflect the larger and not as variable vertical head excursions. Incidentally, the pigeons practically never took a step forwards or backwards during a peck motion, but then the potential target seeds were not scattered enough as to make this necessary.

Figure 1B displays the course of the narrowing and widening of the eyelid slit during the same 30 pecks. It is apparent that the time courses of the slit closure and opening closely parallels the head's approach and withdrawal movements, with the slit widening after seed pick-up sometimes lagging behind by up to as much as 20 ms. The correlation between the motion trajectories of the two nevertheless amounted to an overall $r = 0.73$, with one individual pigeon however exhibiting a noticeably lesser agreement.

Experiment II. Eyelid aperture dynamics

The wide ranging luminances did not appreciably affect the pecking efficiency of the pigeons, which rapidly adapted to them. We assume that the pigeons' vision was in a scotopic state at the two lowest luminances of 1 and 9 lux and it was in a photopic state at all six higher luminances. In more than 90% of all pecks examined in slow motion – many more than those closely analysed – a seed was grasped and swallowed, irrespectively of the luminance level. Note that in the mixed grit-seed condition about 5% of the pecks were clearly not aimed at effecting a seed pick-up and served the purpose of either scattering the particles or ingesting grit (cf. Siemann and Delius, 1992). We only analysed those pecks that led to a seed swallowing.

We noticed that the pupil centre was virtually always located anteriorly (beakwards) with respect to the lateral eyeball aspect and that it frequently appeared slightly elongated in alignment with the beak axis. This was the case despite the fact that at the time of the F2 fixation stop, the pigeons' eyes were turned forward into a convergent position that was not orthogonal

to the camera axis (cf. Wohlschläger et al., 1993), which necessarily yielded a distorted, posteriorly-frontally constricted oval image of the pupil.

The analyses again failed to reveal any peck with completely closed eyelids, a narrow slit always remaining open. From still being wide open during the fixation stop, both eyelids were drawn towards each other somewhat asymmetrically as the head moved downwards from that position. The upper eyelid edge almost always ended up on an eye meridian aligned frontally down by about 20 angular degrees from the beak axis. With a slight delay, the lower eyelid moved upwards to a closely similar position when the slit ended up being narrow; when the slit ended up being wide, the latter eyelid stopped noticeably below the eye meridian. As found in the first experiment, the eyelid slits in virtually all pecks were at their narrowest at the instant when the target seed was being grasped, and thus when their width was measured. These minimum slits were never less than 1.5 mm wide. However, their width was somewhat uneven, the slits being of an elongated ovoid shape, with their broadest extent towards the front, i.e., where the pupil was located due to the convergent forward eye movements. Wider eyelid slits were naturally of a less elongated shape, but still at their widest frontally (Figure 2A). The eyelid edges, by the way, always bulged outwards by about 1.5 mm from the corneal surface.

Whether the eyelid slits encroaching on the pupil opening in turn brought about a reflexive pupil enlargement we are not sure: the instances where the pupil opening was discernible through the eyelid slit indicated that this was not the case. This might be explained by the fact that the pupillary reflex is partly driven by smooth iris muscles and thus exhibits a slower response speed (Alexandridis, 1967; Barbur et al., 2002; Douglas, 2018) than the purely striated eyelid muscles.

Figure 3A plots the mean eye-to-seed distances against luminances. These distances were just significantly affected by luminance levels ($F_{8/32} = 2.8$, $p < 0.02$) and clearly hromati by the seed presentation conditions ($F_{1/4} = 25.9$, $p < 0.01$) but there was no significant interaction between the two factors. The eye-to-seed distances under the seed-only condition (square symbols) were all significantly larger than under the grit-seed condition (triangular symbols), which was to be expected, as this latter condition involved particle discrimination in addition to the aim taking, thus requiring a closer viewing distance (cf. Delius and Delius, 2019). Under the seed-only conditions the eye-to-seed distances increased slightly between 1 and 9 lx but then remained nearly constant at the higher luminances. Under the grit-seed

condition the eye-to-seed distances increased steadily between 1 and 20 lx and then decreased continuously at the higher luminance levels.

Figure 3B plots the pupil openings against the luminance levels under both feeding conditions. They generally decreased in a highly significant manner with increasing luminances ($F_{8/32} = 82.7$, $p < 0.0001$). There was also a significant interaction with the two feeding conditions ($F_{8/32} = 6.3$, $p < 0.0001$) but there was no main effect due to the two conditions. This is in agreement with the fact that the courses of the luminance/width dependences differed under the two conditions. While pupil openings decreased quite steadily under the grit-seed condition with mounting luminances, mostly significantly, the dependence under the seed-only condition evinced a significant local maximum centred around the 60 lx level. Except for this, the pupil openings under the seed-only condition fell off significantly towards the higher luminances, and significantly more steeply than under the grit-seed condition.

Figure 3C plots the eyelid slit widths against the luminance levels under both feeding substrate conditions. Luminances had a highly significant influence on the slit widths ($F_{8/32} = 15.4$, $p < 0.0001$). There was also a significant effect due to the two substrate conditions ($F_{1/8} = 10.8$, $p = 0.01$) but there was no significant interaction between luminance and substrate conditions. There were significant slit width decreases from the 60 lx to 100 lx levels, and the increases from the 300 lx to 5000 lx levels under both conditions were significant in agreement with the overall trough-shaped dependence on luminance levels. There was, however, a significant local minimum at 20 lx under the seed-only condition, a similar but less pronounced minimum not being significant under the grit-seed condition. Except at the 9 lx luminance level, the eyelid slits were all wider under the grit-seed condition than under the seed-only condition.

This difference was significant at four of the eight relevant luminance levels. Note that at the seven luminance levels between 1 lx and 5000 lx, the average slit widths were generally smaller than the pupil diameters, while at 20000 lx luminance the average slit width was greater than the smaller pupil diameter. Both the pupil diameters and eyelid slit widths evince a good deal of variance; this perhaps reflects the fact that both variables are probably also responsive to the emotional state of the pigeons (Bertin et al., 2018).

III. High-speed images

Aperture geometry. Above, we concluded that when the slit width constrained the pupil opening, the aperture effective in terms of light flux would be of an approximately rectangular

shape (slit width × pupil diameter). Regarding depth of focus, the elongated aperture should have a non-isotropic effect in that it would enhance the acuity of retinal image features oriented parallel to the slit elongation but not so much that of features perpendicular to it (cf. Rehkämper et al., 2000). The finding by Lind and colleagues (2008) that homing pigeons – like many other vertebrates with a low depth of focus – possess a multifocal lens arrangement opens up the possibility that the slit formation might improve the visual acuity by reducing chromatic aberration (Kröger et al., 1999). As it constricts, the pigeon's circular pupil would otherwise tend to detract from the benefits of multifocal lensing (Lind et al., 2008). The upward view video recordings were more precisely informative about the slit and pupil geometry determining the effective aperture. The video frame shown in Figure 4C is representative of many more images that we examined. The most salient detail is that the slit widths and pupil diameters of the left eye were consistently larger than those of the right eye. This was due to the different amount of light reaching the two eyes (see Methods section of Experiment II). The asymmetry is due to the fact that the pigeons' pupil responses are not consensually driven like humans' pupil responses (but see Li and Howland, 1999, on chicks), where both pupils always assume an identical midway diameter regardless of any uneven illumination of the two eyes (Gamlin et al., 1984; Bayón et al., 2007); the pigeon's palpebral slit width is obviously also non-consensually driven.

Incidentally, Malmström and Kröger (2006) noted that the pupil of some individual homing pigeons can be somewhat ovally elongated, but did not specify in which orientation. Banks et al. (2015) call attention to the horizontally rectangular pupil of grazing prey animals (e.g., sheep, *Ovis aries*) and the vertical slit pupil of predator animals (e.g., cats, *Felis catus*).

Furthermore, Figure 4C confirms that during the approach phase of pecks, the centres of the pupils are oriented beakwards, in accordance with the increasingly convergent position of the eyeballs. As the pupil of the right eye is relatively small under the 1000 lx luminance, the upper eyelid (Figure 4C) only covers some of the dorsal pupil opening while the lower eyelid does not cover any of the ventral opening. Under the darker 100 lx luminance (Figure 4D), the left eye's pupil is larger and the slit is already narrower, so that the eyelids cover the pupil more symmetrically. The combined pupil-eyelid-slit aperture is thus mostly circle-segment shaped, and only later – when the eyelid slit formation approaches completion – becomes shaped like a mid-circle strip, that is, nearly rectangular. As far as we could observe, the pupil did not dilate when it was partially obscured by the palpebrae, probably because the pupillary reflex is too slow to react to the fast palpebral reflex (see above). The eyelid slit width considered within Experiment II corresponded to those shown here in Figures 4A and B, in that

they rarely reveal the pupil at the instant of seed pick-up. Patently, though, the image of the target grain fell into the middle of the highly resolving 'red' area dorsalis of the retina (Fitzke et al., 1985; Galifret, 1968; Mc Fadden and Wild, 1986; Nalbach et al., 1990).

Nictitating membrane. High-frequency videos taken from below clearly reveal the intervention of the third 'eyelid' that pigeons possess, like many other vertebrates (e.g., cats). These nictitating membranes were not salient in the earlier, slower video takes; even in the single images of the present fast takes they are not very apparent due to the translucence of the membranes. The description that follows is thus based on viewings of the actual videos. The nictitating membranes is drawn across the whole front of the eyeball from the frontal to the posterior eyelid angle (Chard and Gundlach, 1933; Baumel, 1979; Stickney et al., 1981; Burns et al., 2011; Jones et al., 2019). As already noted by Hodos et al. (1976) and Zeigler et al. (1980), the eyelid slit formation during pecking is accompanied by a simultaneous nictitating membrane closure. The nictitating membrane begins to cover the eye front after the final head downward thrust towards the target seed has already began and completely covers the eye front some 70 ms later, the target seed being grasped about 35 ms later. At this stage, the membranes are optically totally transparent; during the initial phase, their forward edges appear to be somewhat milky, probably due to folding and consequent thickness. It is also apparent that as the membranes unfold, a lentiform lacrimal droplet forms within the frontal eyelid corner. Due to this liquid lens the underlying pupil undergoes a noticeable apparent magnification; we are uncertain whether the unfolding nictitating membrane itself additionally contributes to this magnifying effect. We think it is possible that the additional refractive power provided by the droplet ensures that the seed target is kept in focus right up to the seed-grabbing when the eye-to-seed distance has diminished to only about 35 mm. The nictitating membranes then withdraw very rapidly, within some 50 ms.

Discussion

Optical versus protective function. The closure of the eyelids and the nictitating membrane in pigeons doubtlessly has an eye-protective function. Stickney and colleagues (1981; see also Burns et al., 2011) found that 20 psi (=1,38 bar) air puffs directed at a pigeon's cornea would occasion closure of the nictitating membrane. J. D. Delius and V. D. Hollard (1980, unpublished) found that both the palpebral and nictitating membrane reflexes could be triggered by air puffs directed at the pigeon's cornea, though the air pressure required was markedly

higher than that sufficing to elicit the palpebral reflex in humans. Based on this finding and on some contemporary flash photographs by Hans-Jürgen Jahnke, Bochum, of pigeons feeding on mixed seeds on a sandy-powdery substrate, which showed that the bill's impact produced a cloud of scattered grain and grit items, Delius (1985) hypothesized that the eye closure during the terminal phase of foraging pecks was a reflex serving a protective function against backscattering substrate. In Experiment II here, however, the eyelid slits were found to end up being wider under the grit-seed condition than under the seed-only condition. This finding challenges the notion that eye care (corneal wetting and polishing) and protection (preventing particle impacts) are the only functions of the eyelid blinking and the nictitating membrane drawing (see Skalicky, 2016; cf. Sheedy et al., 2003, regarding the depth-of-focus augmenting function of squinting in humans). Incidentally, a further function is revealed by dippers, *Cinclus sps*., which display striking white-flashing eye blinks likely to serve a social signalling function besides eye protection. Their white-feathered eyelids become visible against the background of their dark head feathering when closed and their nictitating membrane appears whitish when only half-drawn (Tyler and Ormerod, 1994).

Returning to pigeons, the fact that a viable aperture remains open across the whole peck cycle indicates that they may make use of visual information throughout its course. The high-speed video recordings in Experiment II showed that seeds and grains of grit scattered by the pigeons' beak impact have typically divergent trajectories and therefore do not really threaten the pigeons' eyes (Figure 5). During the experiments, we never observed any seed or grit-grain hit a pigeon's eyeball or eyelids.

However, J. D. Delius later (2008) obtained clear evidence of eye irritation – repeated eyelid blinks and nictitating membrane draws, wing-bow face-wipings, eye-front foot scratchings – in some trials using finer dust (flour) intermixed with wheat grains, or polenta intermixed with broken maize grains filled into a 5 cm high glass container. More recently, J. D. Delius (2015) observed a small flock of domestic pigeons feeding on seeds dropped within a lawn area with 12× binoculars and saw that they were clearly experiencing eye irritation by the about 4 cm tall grass stalks as they showed similar eye-cleaning responses.

Obviously, a protective function does not need to exclude a parallel optical function of the eyelid squinting/closure response. The slit-like aperture that is approximately aligned with the beak gape can be assumed to increase depth of focus and sharpen the 'edges' of seeds/grains protruding from the beak gape while being swallowed to aid adequate coordination of the pertinent tongue and mandible movements (Banks et al., 2015, their Fig. 2; see also the

"Zirkeln" or "gaping" of common starlings, *Sturnus vulgaris*, Lorenz, 1949; Tinbergen, 1981). Indeed, Experiment IV in Hörster et al. (2002) demonstrated that in effect, active vision definitely goes on during the eye slit-phase in pigeons: an occasionally occurring colour change of the pecking target (a bicoloured light emission diode switch triggered by a head-mounted accelerometer) that occurred well into the eyelid slit phase and signalled that no reward would follow that peck, led to pigeons' interrupting or at least delaying the relevant pecks. In other words, they were able to see the change of colour well after the F2 stop, which was otherwise regarded as the last visual control instance of the forward peck movement. Matsui and Izawa (2018, 2019), somewhat in contrast, found that in comparison to crows (*Corvus macrorhynchos*), pigeons adapt their food-pecking less well when wearing ocular converging prisms or artificially lengthened beaks. They concluded that this may be the case because visual information only accrues at the beginning of pecking in pigeons, whereas this continues at every moment during pecking in crows. Instead, we suggest that the difference may be mainly due to the more 'manipulatively' disposed pecking of crows (dealing with much live prey) and furthermore, to their undoubtedly higher intelligence (Delius and Delius, 2012).

Control by luminance. Earlier we marshalled evidence that the eyelid slit forming during the forward pecking motion, whenever narrow enough, would curtail the circular pupil opening to an almost rectangular aperture, with the area s ≈ d x w. To examine whether this combined aperture depended on the ambient luminance, both under the seed-only and the grit-seed conditions in Experiment II, we estimated the effective apertures under the nine luminance levels according to this simple formula.

The reader must be aware that these are not direct measurements of the apertures because the pupil diameters were those measured at F2, while the slit measurements were those taken at the seed-grasping instant some 35 ms later. We relied on the circumstance that, as pointed out above, the pupillary reflex is slow compared to the speedy eyelid reflex. In future work, it might be helpful to think of the pupil as a dodecaeder inscribed within its outer circumference, wherein the eyelid stripes would take up the form of symmetric trapezoids of a more accurately calculable area.

Figure 6 shows that the estimated net apertures were clearly linearly luminance influenced but rather less dependent on luminance, if at all significantly, in the seed-only than in the grit-seed condition. Whether finer grit than that used here could perhaps enhance this difference remains to be investigated. Recall though that seeds alone were fixated from a greater distance than the grain-grit combination was (Figure 3A). This latter condition doubtlessly

demanded a more careful viewing (it involved an additional discrimination) with a smaller optical aperture to ensure a greater depth of focus (Figure 6).

Conclusion

While not denying the notion that the eyelid part-closures serve an ocular protection function, the evidence presented in this paper strongly suggests that the eyelid slit concurrently serves an optical image sharpening function in agreement with the multifocality of the pigeon's ocular lensing arrangements (Lind et al., 2008). More generally it also strengthens the view that – as has been found to be the case during the rapid head-bobbing while walking (Jiménez Ortega et al., 2009) – pigeons visually steer their voluntary muscular motions even while their heads, and thus their eyes, are moving very rapidly; their vision must thus be quite resistant to motion blur interference (see also Kano et al., 2018, on fast flying among obstacles such as branches). Naturally, the generalization of these findings to other species of birds is fraught with difficulties in view of the variety of their feeding ecologies. How the visual information is converted into peck and grasp muscular commands by neural network processing is yet a further riddle to be solved (Delius and Delius, 2019).

Authors' contributions

J.O. devised the experiments, carried out the experiments, and analysed the results; J.O. and J.D.D. wrote the first drafts. Together with J.A.M.D., they re-edited the present final draft.

Competing interests

The authors declare no competing or financial interests.

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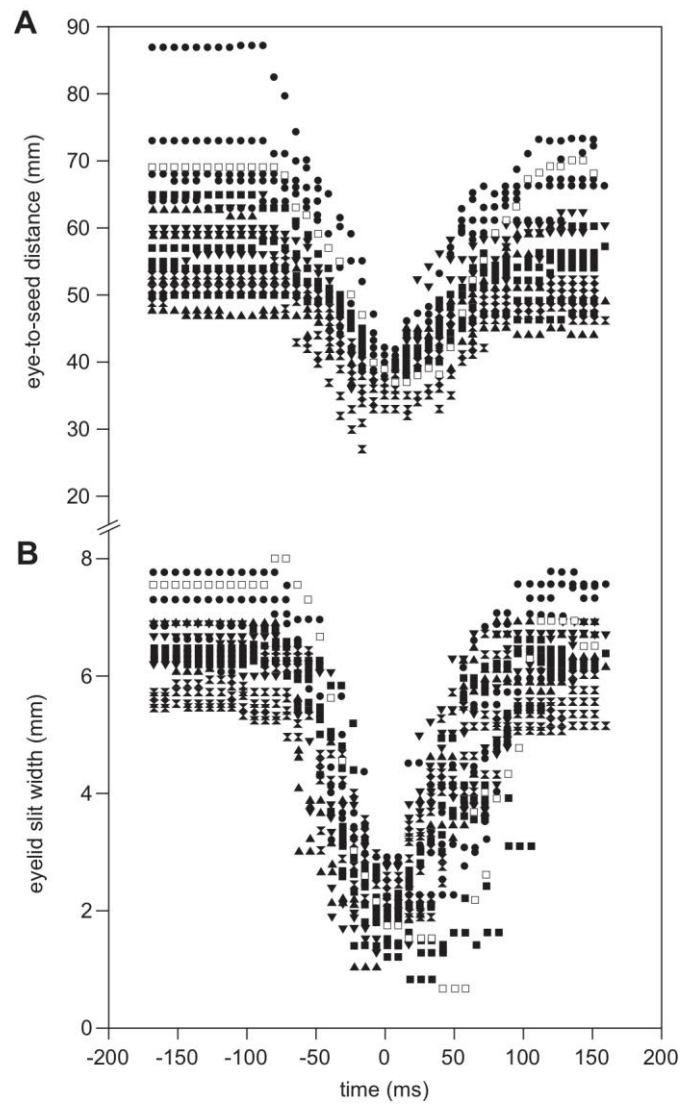
Figures

Figure 1. **The eye-to-target seed distances (A) and the eyelid slit widths (B) during 30 serial pecks.** The five different symbols identify the individual pigeons.
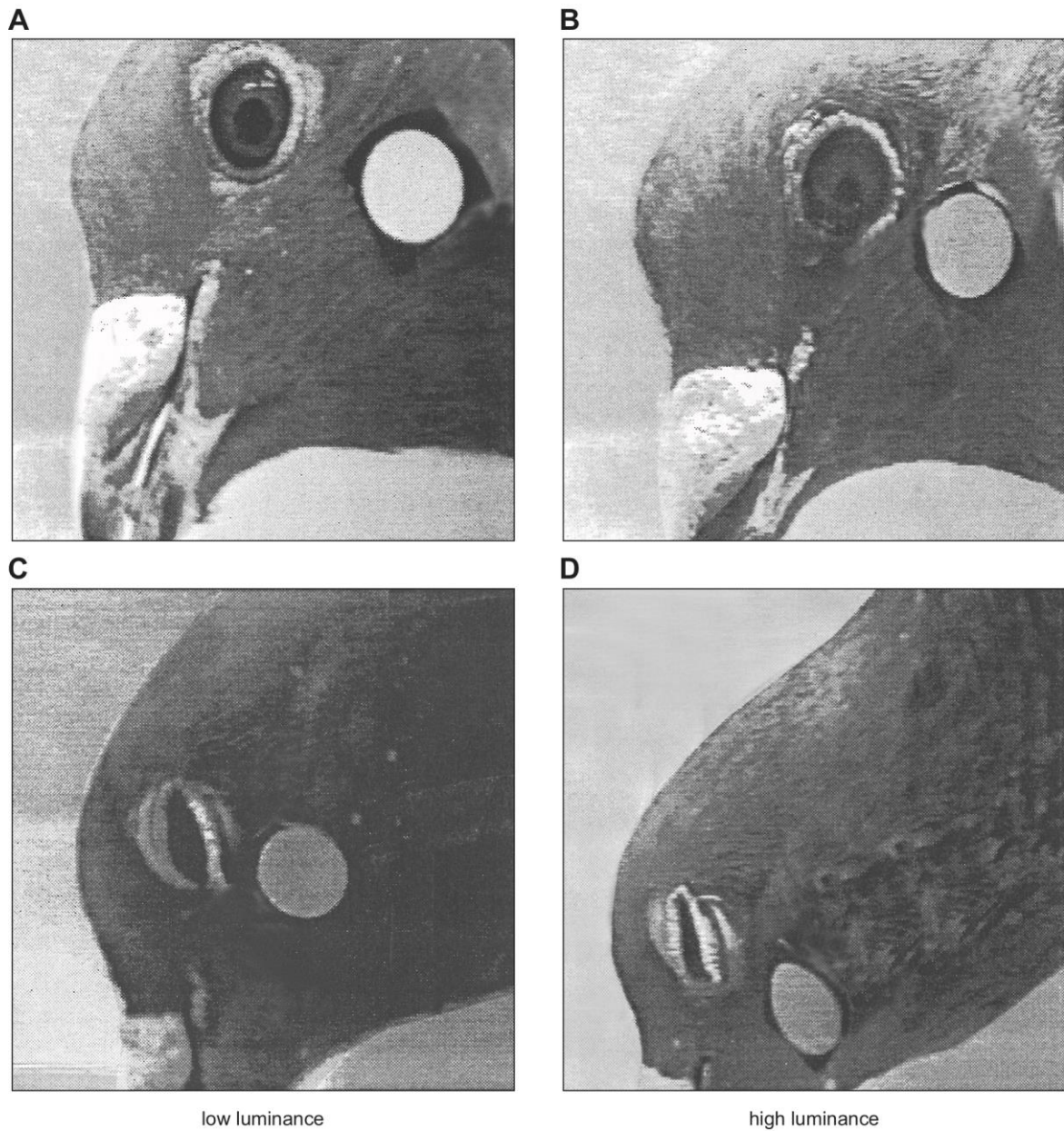
Figure 2. **Pupil openings (A, B) and eyelid slits (C, D) at luminances of 100 lx (left) and 20000 lx (right).** Note that the contrast of the images extracted from the videos was not optimal and had to be increased for illustration purposes.
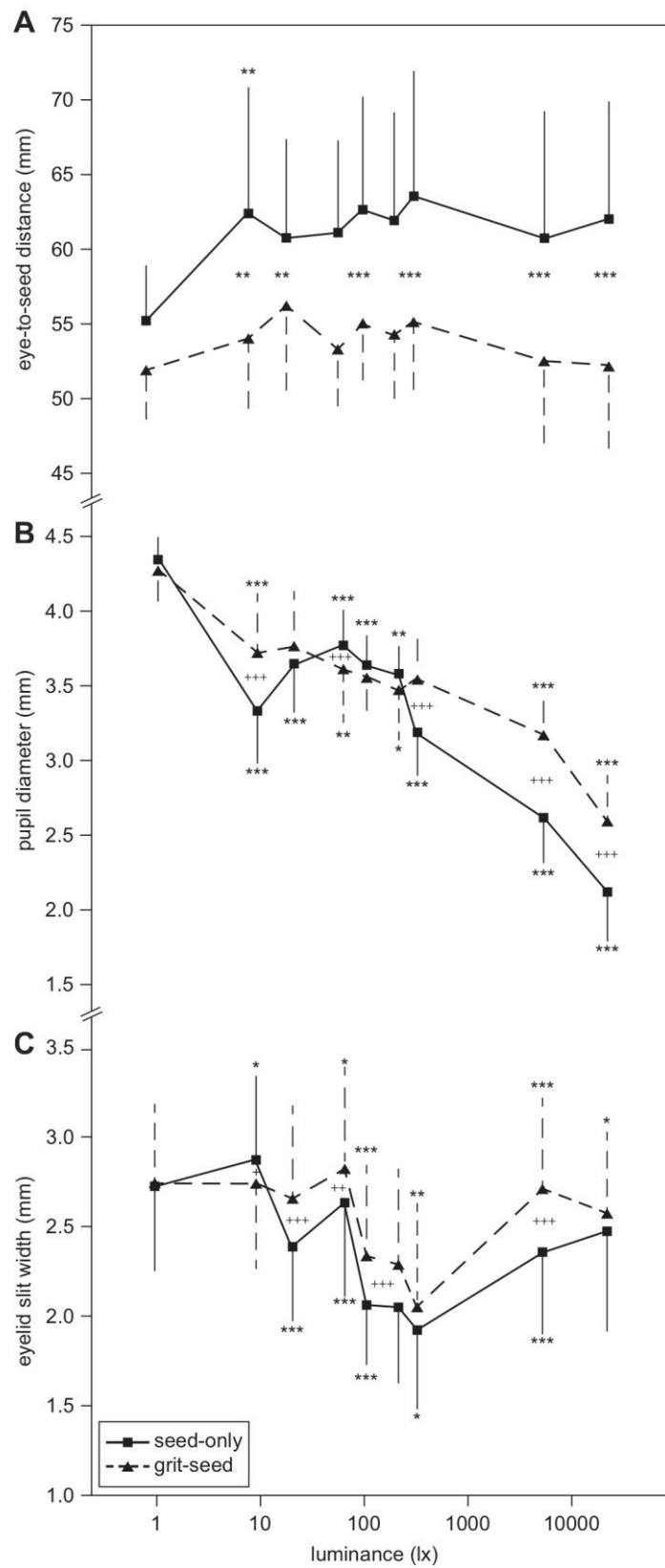
***Figure 3*. Eye-to-seed distances (A), pupil diameter (B), and eyelid slit widths (C).** Separately plotted for the seed-only and the grit-seed conditions against the ambient luminance levels. The means ± standard deviations are all based on the 5 pigeons, 20 pecks each. * denote

significant differences in comparison to the next lower luminance level; $^+$ denote significant differences between the two conditions at a given luminance (*,+ $p < 0.05$, **,++ $p < 0.01$, ***,+++ $p < 0.001$).
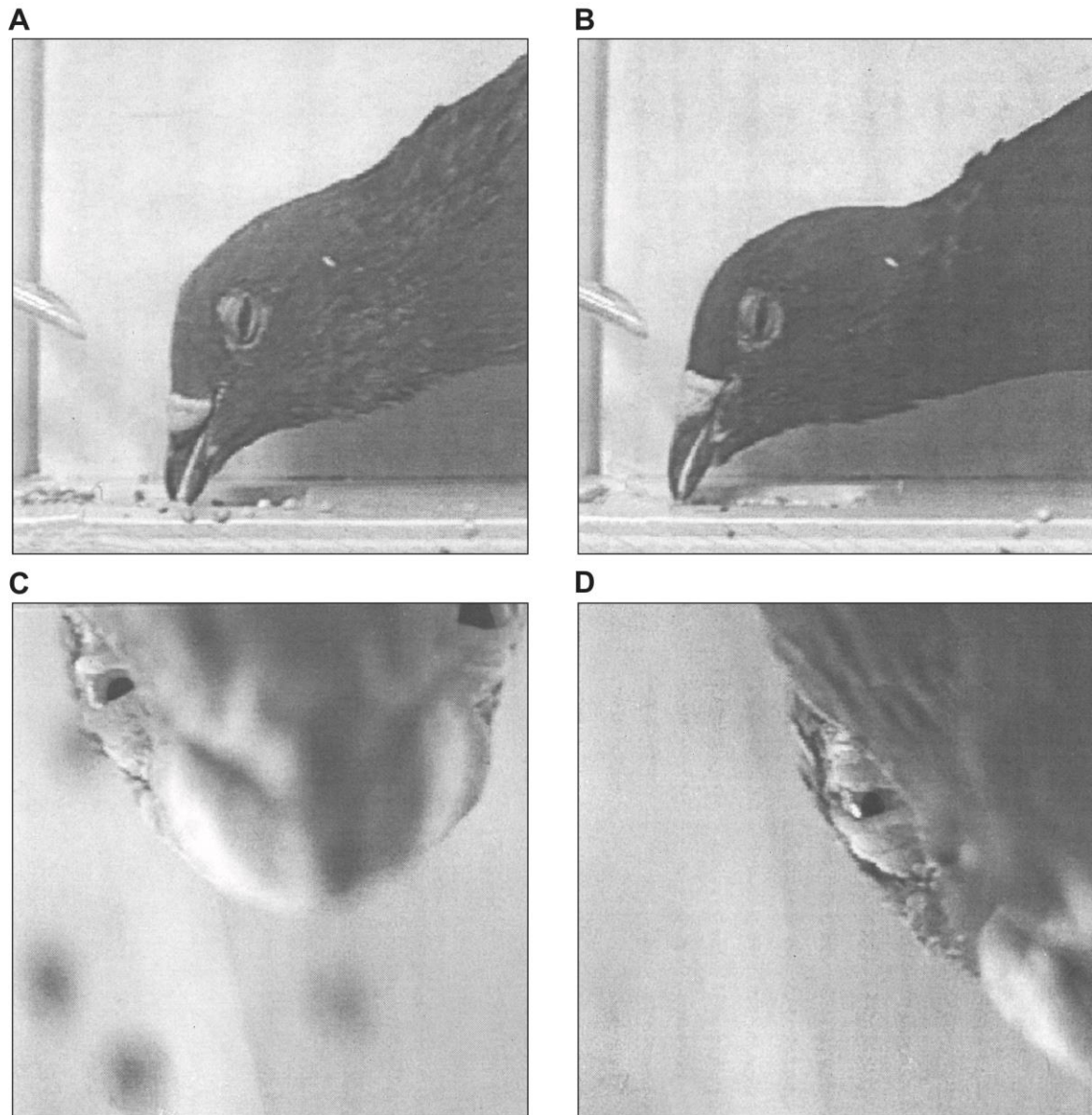
Figure 4. **Pupil and eyelid slit interplay at the instant of seed grasping.** Lateral views from the more highly illuminated side (A, B); ventral views with pigeon's left eye shown on the left (C, D), four different pecks. Note that the contrast of the images extracted from the videos was not optimal and had to be augmented for illustration purposes.
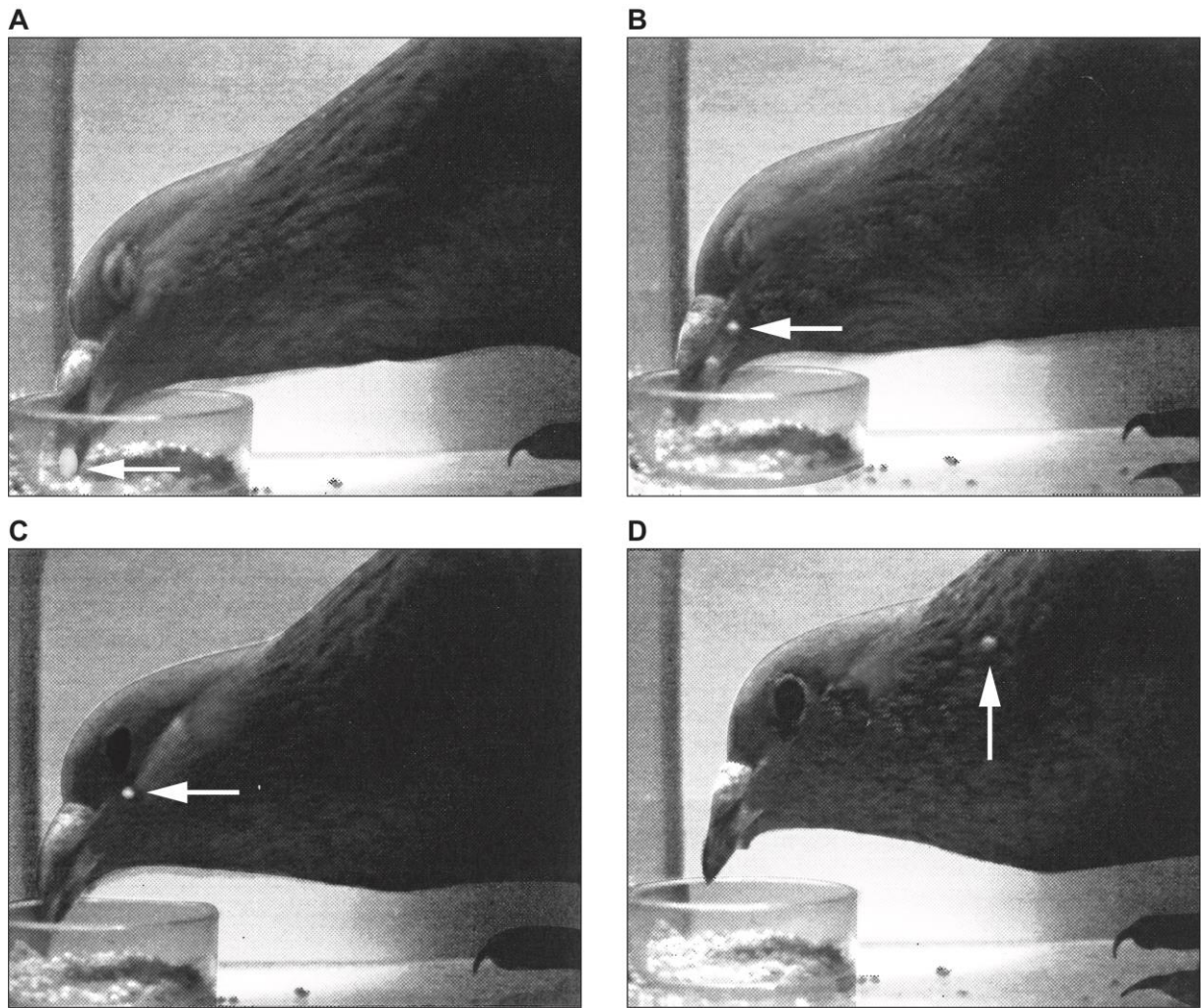
Figure 5. **Seed scattering during the withdrawal phase of a peck (lasting about 125 ms).** Successive images showing a grain flying upwards (A–D, seed indicated by arrow). As before, the contrast of the images extracted from the videos was not optimal and had to be augmented for illustration purposes.
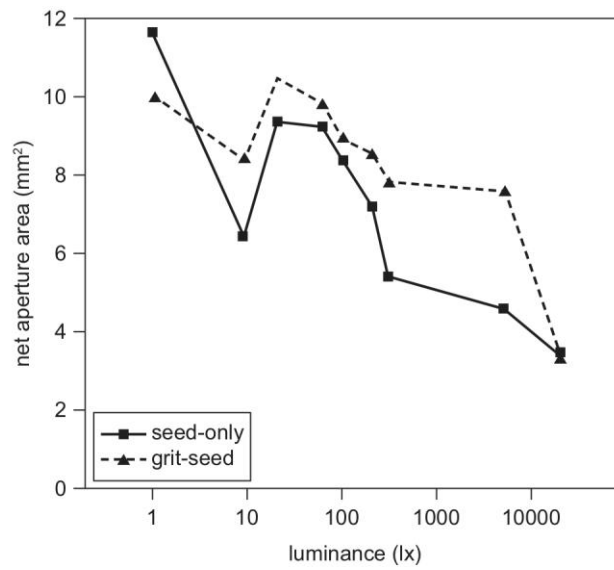
Figure 6. **Estimated effective average apertures (pupil constrained by eyelids).** At the instant of seed grasping under varying luminance levels separately for the seed-only and grit-seed conditions.