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Animal behaviour

A songbird inhibits blinking behaviour in flight

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Visual attention plays a fundamental role in avian flight but attention is likely limited whenever birds blink. Because blinks are necessary to maintaining proper vision, this study tested the hypothesis that birds strategically inhibit their blinks in flight. The blinks of captive great-tailed grackles (*Quiscalus mexicanus*) were recorded before, during and after they flew a short distance in an open environment. The grackles spent the least amount of time blinking in flight (take-off, during flight and landing) and the most amount of time blinking at impact. Their blinking behaviour was similar before and after flight. These results suggest that grackles strategically inhibit their blinking behaviour in flight, potentially because blinks impose costs to avian flight.

1. Introduction

Birds rely strongly on vision during flight [1–3]. They can shift their visual attention in flight by using a combination of their eyes, heads and bodies [4,5]. For example, some species of falcons turn their heads at specific angles relative to their prey while flying, which allows them to fly with their heads pointed straight ahead (therefore minimizing drag) while aligning their foveas with the prey [6,7]. While visual attention is critical in flight, no previous studies have examined how blinking behaviour, a fundamental aspect of visual attention that potentially limits information intake [8], influences it.

The aim of this study was, therefore, to investigate the blinking behaviour of songbirds in flight. Great-tailed grackles (*Quiscalus mexicanus*) are an appropriate songbird species in which to examine this aim because they are adept flyers [9]. Furthermore, they regularly engage in blinking behaviour by sweeping their semi-transparent nictitating membranes across their eyes [10]. The blinking behaviour of captive grackles was recorded before, during and after they flew across a short distance in an open environment. This study tested the hypothesis that grackles strategically modify their blinking behaviour in flight. Because individuals need to be highly alert in flight to avoid collisions, it was predicted that they would inhibit their blinking behaviour the most at take-off and during flight. It was also predicted that they would inhibit their blinks while landing so they can safely terminate flight.

2. Material and methods

The blinking behaviour of captive great-tailed grackles (*Q. mexicanus*) in flight was examined between January and March 2019 (08.00 to 18.00) in College Station, Texas (30.56° N, 96.41° W). Adult birds were captured from the wild in College Station, Texas and surrounding areas. They were housed in outdoor aviaries (2.1 × 2.1 × 1.9 m) and given food (Purina cat chow, Dumor poultry layer feed and dried mealworms) and water ad libitum.

For each trial, a bird was captured from its outdoor aviary (using a butterfly net) and individually transported in a cloth bag to an outdoor testing room (24.4 × 6.1 × 2.1 m; approx. 80 m apart). The bird was outfitted with a camera system that continuously

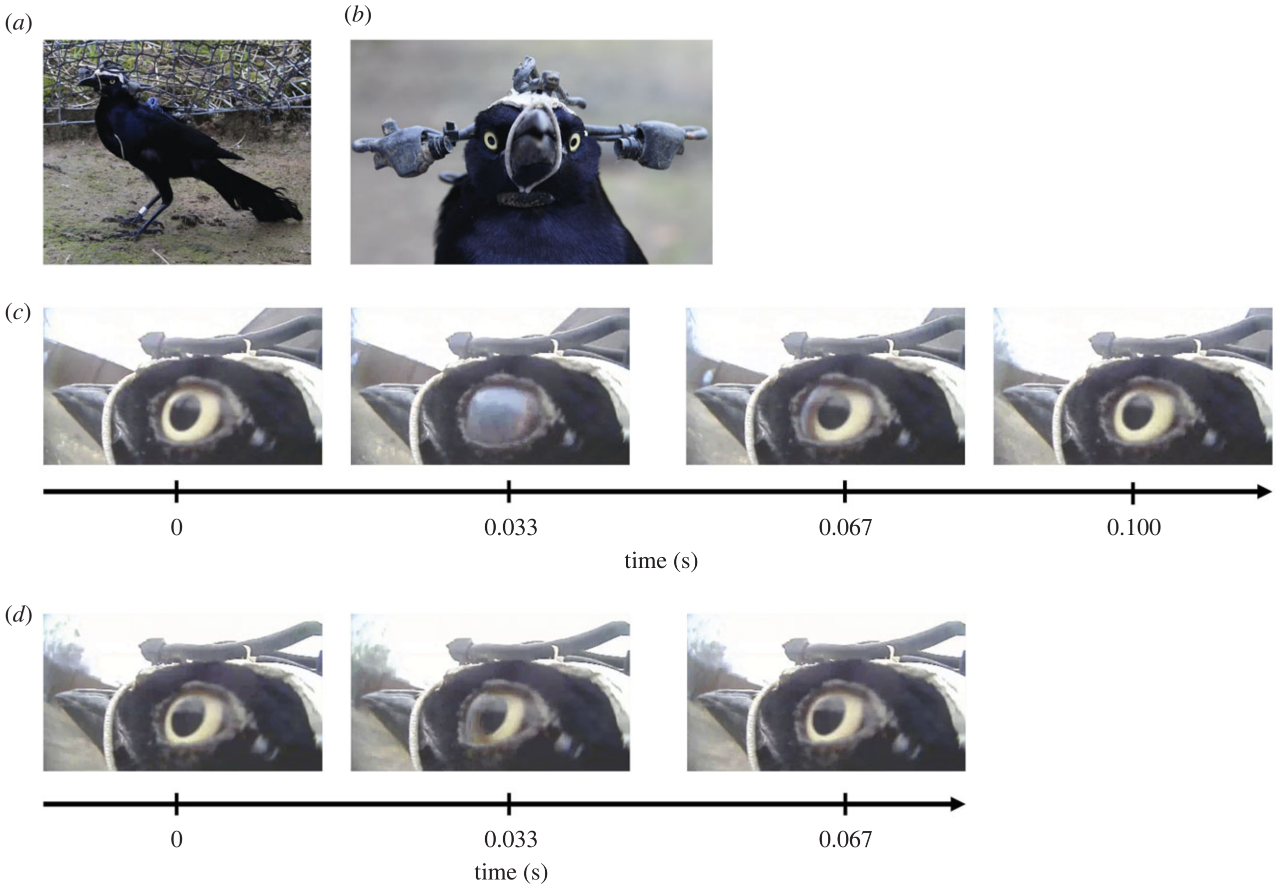

Figure 1. (*a*,*b*) A great-tailed grackle wearing the camera system that continuously records both his eyes. Time series examples of a grackle blinking (*c*) before and (*d*) during flight; the blink lasted 0.067 s before flight and 0.033 s during flight.

recorded its eyes (figure 1*a*,*b*; Positive Science, Inc.). The camera system included a headpiece with two cameras (one camera recorded the bird's left eye and one camera recorded the bird's right eye; 30 fps; 22 g) that was connected to a backpack which contained a transmitter and battery (51 g). Videos from the camera system were transmitted to a nearby computer. The bird was then released into the testing room and given at least 5 min to acclimate. When the bird was located in one corner of the room, the researcher chased him so that he would fly to the opposite side of the room. This was repeated until the bird flew across the testing room at least four times. External video camcorders recorded the testing room. The camera system was then removed from the bird and the bird was returned to the aviary. The temperature, relative humidity and wind speed as well as the light level and mass of the bird were measured immediately after each trial. Ten adult males were tested (females were too small to wear the camera system). Trials were conducted on overcast days that were not windy (wind speed was 0 m s^{-1} in all trials). The temperature (mean ± s.e.: 18.5 ± 1.6°C; range: 9.1–25.3°C), relative humidity (mean ± s.e.: 76.0 ± 5.8%; range: 51.0–97.0%), light level (mean ± s.e.: 8.3 ± 1.4 klx; range: 1.8–15.8 klx) and bird mass (mean ± s.e.: 211.3 ± 4.5 g; range: 190.5–239.7 g) varied across trials. Because of technological limitations, the camera system was limited to capturing videos at 30 fps, which was a relatively low sampling rate compared with the average blink duration (mean ± s.e.: 0.067 ± 0.0006 s). However, our previous work found that grackle blinks rarely (less than 0.01% of blinks) last less than 0.033 s [10].

The blinking behaviour of the birds was measured from the videos using Quicktime (Apple, Inc.). All of the videos from a given trial were synchronized and clips were extracted from each of the four times the bird flew across the testing room after being chased. In addition, the bird sometimes flew across the testing room without being chased and up to four clips from these flights were also extracted. Each clip included flight stages before, during and after the bird flew. The 'before' flight stage included the 10 s immediately preceding the flight start while the 'after' flight stage included the 10 s immediately after the flight end. The flight start was defined as the first frame when the bird's feet were no longer touching the ground; the flight end was defined as the first frame the bird's feet contacted the landing surface. The flight stages also included 'take-off' (the first 0.33 s of flight), 'during' (the time between 'take-off' and 'landing'), 'landing' (the 0.33 s immediately preceding the 'impact') and 'impact' (the 0.10 s before the flight end as well as the 0.033 s when the bird's feet contacted the landing surface). The duration of the total flight time (flight end minus flight start) varied across birds (mean ± s.e.: 3.0 ± 0.05 s; range: 2.0–3.93 s). The 'take-off' and 'landing' flight stages each lasted 0.33 s (approx. 10% of the total flight time) in order to capture a brief time period at the beginning and ending of flight. The 'impact' flight stage conservatively included the 0.10 s immediately before the birds contacted the landing surface as well as when the birds contacted the landing surface to account for potentially minor inaccuracies (due to the position and resolution of the external camcorders) in the exact moment when the birds' feet first touched the landing surface.

For each trial, the frame at which each blink began and ended during the clip was recorded (figure 1*c*,*d*). Using customized scripts (Matlab; Mathworks, Inc.), the blink rate, blink duration and percentage of time spent blinking were calculated for each flight stage (electronic supplementary material, S1 methods). In the before flight stage (using the left eye), the number and amplitude of saccades were also quantified (because of slight shifts in the camera system, only eye movements above 3° were classified as saccades) using previously established methodology that measured the distance that the eyes moved in the vertical and horizontal planes [5].

Table 1. The effect of flight stage, chase, temperature, relative humidity, and light level on blink rate, blink duration, and percentage of time spent blinking. *F*-values are displayed for the overall model and *t*-values are displayed for the comparisons; *p*-values are indicated in parentheses and statistically significant comparisons are indicated with an asterisk. The degrees of freedom for blink rate and time blinking are listed first and the degrees of freedom for blink duration are listed in parentheses, if they differ.

	numerator d.f., denominator d.f.	blink rate (blinks min^{-1})	blink duration (s)	time blinking (%)
overall model				
flight stage	4, 36	160.49 (<0.0001)*	74.85 (<0.0001)*	325.71 (<0.0001)*
chase	1, 5	2.36 (0.19)	3.81 (0.11)	0.44 (0.54)
flight stage × chase	4, 20 (4, 18)	1.37 (0.28)	1.49 (0.25)	0.69 (0.61)
temperature	1, 6	4.34 (0.082)	1.17 (0.32)	1.4 (0.28)
relative humidity	1, 6	0.07 (0.81)	6.89 (0.039)*	6.62 (0.042)*
light level	1, 6	1.04 (0.35)	2.73 (0.15)	0.27 (0.62)
comparisons				
before versus take-off	1, 36	5.01 (<0.0001)*	7.28 (<0.0001)*	8.63 (<0.0001)*
before versus during	1, 36	0.47 (0.64)	9.06 (<0.0001)*	4.91 (<0.0001)*
before versus impact	1, 36	15.43 (<0.0001)*	6.27 (<0.0001)*	20.65 (<0.0001)*
before versus after	1, 36	0.81 (0.42)	0.36 (0.72)	0.51 (0.62)
take-off versus during	1, 36	5.44 (<0.0001)*	0.36 (0.72)	4.59 (<0.0001)*
take-off versus impact	1, 36	17.21 (<0.0001)*	12.07 (<0.0001)*	20.99 (<0.0001)*
take-off versus after	1, 36	4.26 (0.0001)*	7.56 (<0.0001)*	8.24 (<0.0001)*
during versus impact	1, 36	15.21 (<0.0001)*	15.32 (<0.0001)*	22.35 (<0.0001)*
during versus after	1, 36	1.29 (0.21)	9.42 (<0.0001)*	4.41 (<0.0001)*
impact versus after	1, 36	15.9 (<0.0001)*	5.91 (<0.0001)*	20.76 (<0.0001)*

The data were analysed using generalized linear mixed models in SAS (PROC GLIMMIX). I analysed 40 clips when the birds were being chased (10 birds, 4 flights each) and 16 clips when the birds were not being chased (6 birds, 1–4 flights each). The blinking variables (blink rate, blink duration and percentage of time spent blinking) were used as the dependent variables. The blink rate and percentage of time spent blinking were analysed using a Poisson distribution while the blink duration was analysed with a normal distribution. The independent variables were the flight stage (before, take-off, during, impact, after), chase (whether or not the experimenter chased the bird), the interaction between flight stage and chase, as well as the ambient temperature, ambient relative humidity and light level. Bird identity (random factor) was included within the model to account for repeated measures. *A priori* contrasts were performed to compare the blinking variables among flight stages; 10 comparisons were performed and the false discovery rate correction was used to evaluate statistical significance (the false discovery rate was controlled at $q^* = 0.05$; [11]). It was not possible to include blinks from the 'landing' flight stage within these models because the birds rarely blinked during this stage (only two birds blinked); therefore, Wilcoxon signed-rank tests were performed to compare blink rate and percentage of time spent blinking in the 'landing' flight stage compared with the other flight stages (blink duration was not analysed because of the limited number of blinks in the 'landing' flight stage).

3. Results

The birds modified their blinking behaviour relative to the flight stage (table 1; figure 2; electronic supplementary material, figure S1 and movie S1). Their blink rate before, during and after flight was similar but they exhibited a lower blink rate at take-off and higher blink rate at impact (table 1: blink rate). Furthermore, the blink rate was lower at landing compared with all of the other flight stages (electronic supplementary material, table S1: $p < 0.0001$; figure 2*a*). While their blink duration was similar before (figure 1*c*) and after flight, their blink duration was lowest at take-off and during flight (figure 1*d*) and highest at impact (table 1: blink duration; figure 2*b*). In fact, blinks never lasted more than 0.067 s at take-off, 0.10 s during flight or 0.033 s at landing but lasted up to 0.37 s before flight, 0.27 s at impact and 0.63 s after flight. The time they spent blinking before and after flight was similar; however, they spent less time blinking at take-off and during flight and more time blinking at impact (table 1: time blinking). In addition, the time they spent blinking was lower at landing compared with all of the other flight stages (electronic supplementary material, table S1: $p < 0.0001$; figure 2*c*). The temperature, relative humidity and light level did not impact blinking behaviour except that the blink duration and percentage of time spent blinking were lower when the relative humidity was higher (table 1). Blinking behaviour was not influenced by whether the experimenter was or was not chasing the bird ($p > 0.10$). The results were qualitatively similar when the analysis was performed on a composite blinking variable (blink rate, blink duration and percentage of time spent blinking; electronic supplementary material, S1 methods, tables S2–S4 and figure S2). Lastly, 33% of saccades ($n = 909$) were not associated with blinks and 35% of blinks ($n = 951$) were not associated with saccades. Saccade amplitude was unrelated to whether the birds blinked or not ($F_{1,9} = 1.20$, $p = 0.30$).

4. Discussion

These results support the hypothesis that great-tailed grackles strategically modify their blinking behaviour in flight. The

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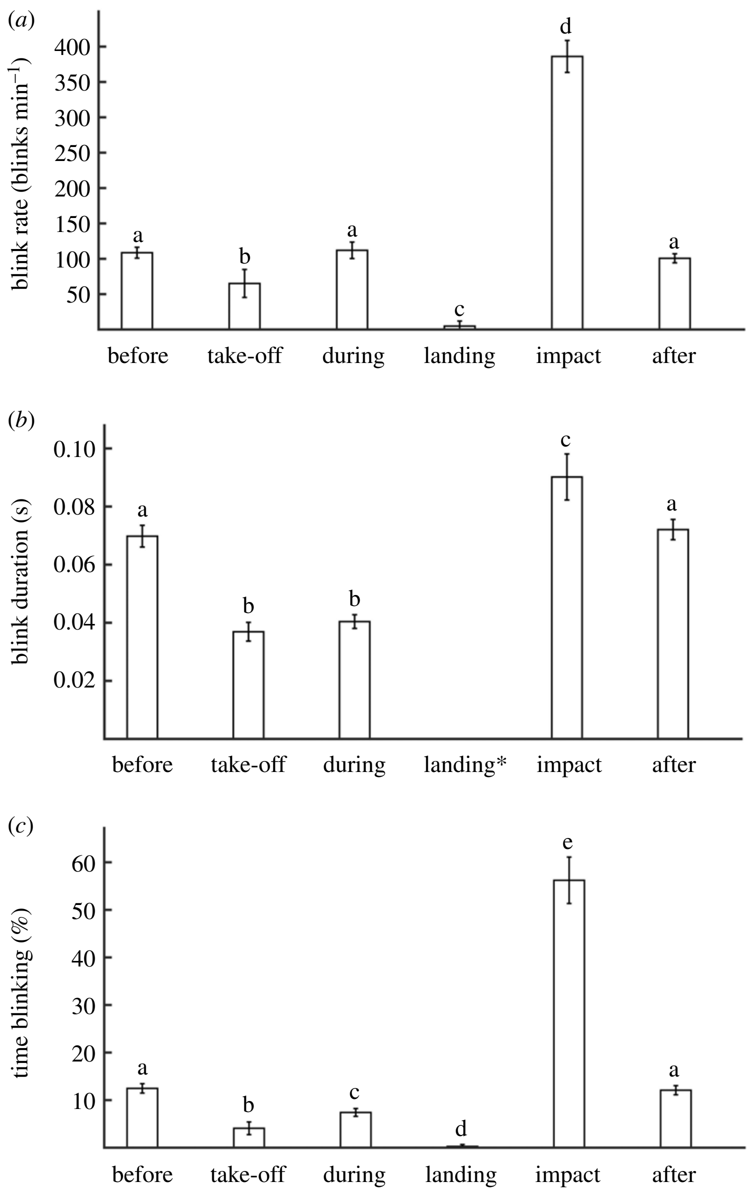

Figure 2. The (*a*) blink rate, (*b*) blink duration and (*c*) percentage of time spent blinking relative to flight stage ($n = 10$). Means and 95% confidence intervals are displayed. Flight stages with different letters are statistically different based on the generalized linear mixed models and Wilcoxon signed-rank tests. *Because the birds rarely blinked in the 'landing' flight stage, blink duration in this flight stage was not analysed.

grackles spent the least amount of time blinking at take-off, during flight and at landing. They spent the most amount of time blinking at impact. Their blinking behaviour was similar before and after flight.

By limiting the amount of time they spent blinking in flight (take-off, during flight, and landing), the grackles were potentially maximizing their information uptake. Because of the semi-transparent nature of their nictitating membrane, the grackles probably experience visual impairments during blinks. Furthermore, it is also possible that their neural activity is suppressed during blinks, as demonstrated in humans [12,13]. Therefore, by minimizing the time they spend blinking, the birds are likely maximizing the visual input they receive from their environments. However, it is possible that birds can compensate for any costs associated with blinking behaviour by using specialized neural processing abilities or performing behavioural adjustments. Because flying is dangerous owing to the risk of collisions [14,15] and landing safely [16], it is especially important for birds to remain alert in flight. Similarly, pilots exhibit shorter blinks and blink less often during flight and landing [17,18]. Future experiments could test whether avian blinking behaviour is inhibited more in cluttered environments compared with open environments given that the risk of collision is higher in cluttered environments.

Because birds inhibit their blinks when under threat [19–21], it is possible that the grackles inhibited their blinks in flight because they were threatened by the experimenter. However, blinking behaviour was not influenced by whether the experimenter was chasing them or not, suggesting that threats were not the driving influence of their blinking behaviour. Alternatively, grackles may have spent less time blinking in flight because of their eye movement patterns. In some species, blinks are strongly associated with saccades [20,22] and grackles may have spent less time blinking in flight because they were making fewer saccades [23]. However, blinks and saccades are not very strongly related in grackles: 33% of saccades were not associated with blinks and 35% of blinks were not associated with saccades.

Interestingly, the blink duration was relatively brief in flight. These blinks were often so brief that the nictitating membrane did not sweep across the entire eye. In such instances, the nictitating membranes could partially lubricate the eyes or clear foreign debris while minimizing visual interference. Future studies that use cameras with higher frame rates to record blinking behaviour would provide finer precision in evaluating blink duration. By contrast, the grackles increased their blink rate and blink duration at impact. They may have increased their blinking behaviour to protect their eyes from foreign debris at impact with the landing surface or compensate for briefer blinks during flight [8]. Additional studies could directly test whether grackles increase their blinking behaviour when exposed to foreign debris by manipulating the type of landing substrate. To my knowledge, these results provide the first evidence to suggest that birds strategically modify their blinking behaviour in flight. Future experiments that examine the costs associated with blinking will provide additional insight into the evolution of visual processing during complex locomotion across species with different sensory systems.

Ethics. This work was approved by the Texas A&M University Institutional Animal Care and Use Committee (no. 2019-0219), Texas Parks and Wildlife Department (SPR-1116-279), United States Fish and Wildlife Service (MB160637-0 and MB47977D-0) and United States Geological Survey Bird Banding Laboratory (24067).

Data accessibility. Data are available in the electronic supplementary material.

Competing interests. I declare I have no competing interests

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