Received: 7 October 2019 | Revised: 19 December 2019 | Accepted: 23 December 2019

DOI: 10.1111/eth.13003

RESEARCH PAPER

ethology WILEY

Blinking behavior in great-tailed grackles (*Quiscalus mexicanus*) increases during simulated rainfall

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Abstract

Animals often adjust their behavior in response to changes in environmental conditions, and these behavioral adjustments may result from sensory constraints. In particular, rainfall influences behavior but our understanding of its effects on visual abilities is limited. This study, therefore, tested the hypothesis that rainfall influences blinking behavior, a major component of visual processing, in captive great-tailed grackles (*Quiscalus mexicanus*). The blinking behavior of the grackles was recorded when they were exposed to simulated rain that was direct (water falling directly atop them) or indirect (water falling at a distance from them). The grackles exhibited increased blinking behavior when they were exposed to the direct rain but not the indirect rain. These results suggest that rainfall may impact visual processing in birds through sensory impairments.

KEYWORDS

attention, eye blink, head movement, rainfall, weather

1 | INTRODUCTION

Animals often alter their behavior relative to abrupt changes in environmental conditions (Boyle, Norris, & Guglielmo, 2010; Streby et al., 2015). In particular, rainfall can influence behavior as many species change their activity patterns in response to rain (Belwood & Fullard, 1984; He, Tian, Wu, & Zeng, 2016; Kennedy, 1970). For example, many songbirds and bats seek cover during heavy rain (Belwood & Fullard, 1984; Hume, 1986; Kennedy, 1970; Robbins, 1981). Similarly, avian predators also remain in cover during rain (Sergio, 2003; Touchton, Hsu, & Palleroni, 2002). In contrast, mammalian predators increase their activity levels in rainy conditions (Jenny & Zuberbühler, 2005; Koshkarev, 1984). Species clearly vary in their behavioral responses to rainfall, but our understanding of this variation is limited.

Physiological responses may underlie behavioral variation among species in their responses to rainfall. In particular, rainfall often increases metabolic costs. During brief flights, Sowell's short-tailed fruit bats (*Carollia sowelli*) and Anna's hummingbirds (*Calypte anna*) have high metabolic rates when exposed to rain (Voigt, Schneeberger, Voigt-Heucke, & Lewanzik, 2011). Bald eagles (*Haliaeetus leucocephalus*), American kestrels (*Falco sparverius*), and European rabbits (*Oryctolagus cuniculus*) also exhibit high resting metabolic rates when experiencing rainy conditions (Seltmann, Ruf, & Rödel, 2009; Stalmaster & Gessaman, 1984; Wilson, Cooper, & Gessaman, 2004). The high metabolic rates are likely due in part to heat loss during wetting (Webb & King, 1984; Wilson et al., 2004), which is particularly pronounced for individuals with small body sizes (Müller & McCutcheon, 1991). Given high metabolic costs during rainfall in some species, individuals that minimize their behavioral activity during rainy conditions may maximize their energetic tradeoffs. Interspecific interactions could also underlie altered behavior during rainfall. Potentially due to shifts in prey availability during rainfall, avian predators often stop hunting during rain (Sergio, 2003; Touchton et al., 2002) while mammalian predators hunt more often in rainy conditions (Jenny & Zuberbühler, 2005; Koshkarev, 1984). Rainfall may also impact sensory abilities (Hilton, Ruxton, & Cresswell, 1999; Koshkarev, 1984; Voigt et al., 2011). Rainfall might impair auditory abilities such that prey cannot easily detect approaching predators (Hilton et al., 1999; Koshkarev, 1984).

It might also interfere with echolocation and limit predators' abilities to target prey or avoid obstacles (Voigt et al., 2011). Furthermore, rainfall may reduce visibility by limiting visual processing. Despite the possibility that rainfall impacts visual abilities, no studies have directly tested this hypothesis.

The aim of this study was, therefore, to test the hypothesis that rainfall influences blinking behavior, a fundamental aspect of visual processing (Sweeney, Millar, & Raju, 2013). Blinking behavior is necessary to maintaining clear vision but individuals likely experience impaired visual processing during blinks (Bristow, Haynes, Sylvester, Frith, & Rees, 2005; Hoppe, Helfmann, & Rothkopf, 2018; Volkmann, Riggs, & Moore, 1980). Indirect evidence suggests that blinking behavior in birds interferes with visual processing because birds strategically inhibit their blinks (Beauchamp, 2017; Cross et al., 2013; Yorzinski, 2016) and the nictitating membrane used for blinking is only semi-transparent in many avian species (Sivak, 1980). The impact of simulated rainfall on blinking behavior was tested using captive great-tailed grackles (*Quiscalus mexicanus*), a songbird species that often inhabits open areas in regions with periodic rainfall (Johnson & Peer, 2001). Grackles blink by sweeping their semi-transparent nictitating membranes across their eyes, but their eyelids generally remain open when they are alert. The blinking behavior of the birds before, during, and after they were exposed to simulated rain that was falling directly atop them was recorded. Because factors associated with rainfall aside from water exposure (e.g., changes in relative humidity or sound generated by falling water) could potentially impact blinking behavior, their blinking behavior before, during, and after they were exposed to simulated rain that was falling at a distance from them was also recorded. The birds were tested when their heads were restrained and unrestrained; because blinks often coincide with head movements in many species (Beauchamp, 2017; Evinger et al., 1994; Gandhi, 2012; Yorzinski, 2016), the effect of rainfall on blinking behavior could be examined without the possible confounding effect of head movements by restraining the birds' heads. Blinking behavior was expected to increase when the birds were exposed to the direct rain (but not the indirect rain) because ocular irritants generally increase blinking behavior (Nakamori, Odawara, Nakajima, Mizutani, & Tsubota, 1997; Wu, Begley, Situ, & Simpson, 2014; Yang, Zhang, Chen, Chen, & Wang, 2001; Yorzinski & Argubright, 2019) and raindrops remaining on the eye surface might obscure vision.

2 | METHODS

2.1 | Study site and animal subjects

The impact of rain on blinking behavior in captive great-tailed grackles (*Q. mexicanus*) was studied between July and October 2018 in College Station, Texas (30.56°N, 96.41°W). Adult birds (*n* = 36) were captured from the wild in College Station, Texas, and housed in outdoor aviaries (2.1 × 2.1 × 1.9 m) with one to ten other conspecifics (males and females). They were given food (Purina cat chow, Dumor poultry layer feed, and dried mealworms) and water ad libitum. The study was approved by Texas A&M University's Animal Care and Use Committee (#2016-0250).

2.2 | Experimental procedure

For each trial, a bird was captured from its outdoor aviary (using a butterfly net) and individually transported in a cloth bag to an indoor cage (0.76 × 0.46 × 0.46 m; approximately 160 m apart). The bird remained within this cage for at least 30 min so that it could acclimate to being indoors (food and water were provided ad libitum). After this acclimation period, the bird was placed inside a testing arena and secured to a foam cradle using velcro straps. The testing arena consisted of the area within a large plastic box (0.6 × 1 ×0.7 m; Wolverine model cooler; Iowa Rotocast Plastics, Inc., Decorah, IA). An LED light strip on the roof of the cooler provided lighting (2.2 kLux; light meter positioned directly upward at the location of the foam cradle; Easyview 31; Extech Instruments, Waltham, MA). In head-restrained trials, the bill of the bird was fastened to a wooden dowel (using narrow strips of tape; Gorilla Glue, Inc.) that was secured to the testing arena floor (0.14 m high) to prevent the bird from moving its head; in head-unrestrained trials, the wooden dowel was not present and the head of the bird could freely move.

In the head-restrained trials, two video cameras (60 frames/s; VIXIA HF R70; Canon, Inc.) were located on opposite sides of the bird to record each eye. The bird was simultaneously monitored in real time using camcorders (SRPRO-T855CAM; Swann Communications) multiplexed to a DVR (model 2600; Swann Communications). In the head-unrestrained trials, another camcorder (60 frames/s; VIXIA HF R70; Canon, Inc.) was also placed behind the bird so its eyes could be recorded if it turned its head backward. In addition, another two camcorders with higher frame rates (240 frames/s; Hero 5; GoPro, Inc.) were positioned on either side of the bird. The ambient temperature and relative humidity inside the testing arena were continuously recorded (1 s interval; HOBO MX2301; Onset Computer Corporation).

Each bird was exposed to two treatments: direct rain and indirect rain. During the direct rain treatment, a showerhead (Forte; Kohler, Inc.) connected through a hose to a water faucet was attached to the roof of the testing arena directly above the bird and sprinkled water on the bird. During the indirect rain treatment, the showerhead was attached to the roof of the testing arena 0.4 m in front of the bird and sprinkled water but none of the water fell on the bird. The indirect rain treatment was performed to determine whether water falling directly atop the bird rather than other factors (such as changes in relative humidity, noise from the falling water, stress of being restrained, or presence of nearby water) influenced blinking behavior. During both treatments, the water was remotely programmed (water timer BO9DB; Dig Corporation, Vista, CA) to sprinkle water for one minute after the bird had been inside the testing arena for five minutes. Each bird was removed from the foam cradle one minute after the water stopped. The bird was then returned to its outdoor aviary. The showerhead (diameter: 0.14 m; 72 spray holes) released 375 ml of water per minute, and the water was slightly warmer (26°C) than the mean ambient temperature (mean ± SE: 22.0 ± 0.10°C). The 72 spray holes were distributed along four concentric circles within a 0.1 m diameter area of the showerhead such that the holes were each separated by approximately 0.01 m. The water droplets fell at approximately 1.5 m/s. Given that natural rain droplets fall at velocities up to 9 m/s (Gunn & Kinzer, 1949), the simulated rain droplets fell at velocities toward the slower range of natural raindrops. Using a graduated cylinder rain gauge, the simulated rainfall intensity was measured as approximately 80 mm/min, which would be classified as torrential rainfall (King, Portabella, Lin, & Stoffelen, 2017). At least 5 days lapsed between treatments (indirect rain or direct rain) for a given bird, and treatment order was randomized across birds. Each bird was either tested in the head-restrained or head-unrestrained trials for both treatments. Fifteen females in the head-restrained trials and 15 females in the head-unrestrained trials were tested; four males in the head-restrained trials and two males in the head-unrestrained trials were tested. One of the males and one of the females in the head-restrained trials were only tested in one treatment because the birds died unexpectedly before being tested in the second treatment. More females were tested compared with males because of logistical difficulties in capturing males from the wild.

2.3 | Behavioral coding and interobserver reliability

The blinking behavior of the birds was measured from the videos using Quicktime (version 7; Apple Inc.; Figure 1). All of the videos from a given trial were synchronized, and a three-minute clip was extracted from each trial that included three time periods: a one-minute period before the water turned on, a one-minute period while the water was turned on, and a one-minute period after the water turned off. For each trial, the frame at which each blink began and ended during the three-minute clip was recorded. A blink start was defined as the first frame when the nictitating membrane covered the pupil (or part of it), and the blink end was defined as the first frame when the nictitating membrane was no longer covering any part of the pupil. The blink start and blink end were defined in relation to the pupil because the nictitating membrane would often remain slightly exposed in the corner of the eye during the direct rain (but not indirect rain); given that the nictitating membrane was only slightly exposed and not covering the pupil in these instances, these times were not considered blinks so that blinking behavior could be compared between the direct and indirect rain treatments. In cases when the nictitating membrane was not continuously shut (e.g., the nictitating membrane completely covered the eye but then retracted slightly but still covered part or all of the pupil), a single blink was scored. The blinks in the left and right eye were recorded separately because the birds did not always synchronize their blinks between the eyes. In the head-unrestrained trials, the videos that were recorded at the higher frame rate were consulted to score the blinks when the birds moved their heads quickly (their eyes were sometimes blurred using the videos with the lower frame rate during quick head turns, so blinks sometimes needed to be confirmed using the videos with the higher frame rate).

To ensure reliability in coding the blinking behavior, each of the three coders practiced their scoring methods on a video from one of the trials. After an initial training period in which they scored twenty blinks and received feedback on their scoring from a trainer (JLY), they scored another twenty blinks and these blinks were compared with those scored by the trainer. The blinks from the coders and the trainer were scored similarly (over 90% of the blinks of each coder were scored in the same way as the blinks scored by the trainer).

For the head-unrestrained trials, headshaking was also scored (by a single coder: JLY). Headshaking was defined as when the birds rapidly moved their heads from side to side, a behavior observed in other avian species under rainy conditions to expel water (Ortega-Jimenez & Dudley, 2012).

2.4 | Blink metrics

Using customized scripts (Matlab; Mathworks, Inc.), the blink rate, blink duration, percentage of time spent blinking, and percentage of synchronized blinks were calculated for each time period. The blink rate was calculated as

$$\frac{(\#\textit{of left eye blinks} + \#\textit{of right eye blinks})/2}{\textit{time period}}$$

The blink duration was calculated as

$$\frac{\textit{mean duration of each left eye blink} + \textit{mean duration of each right eye blink}}{2}$$

The percentage of time the birds spent blinking was calculated as

$$\frac{\%\textit{ of time left eye blinking} + \%\textit{ of time right eye blinking}}{2}$$

The percentage of time the birds were synchronizing their blinking behavior was calculated as

$$\left(\frac{\#\textit{ of frames left and right eye both blinking or both not blinking}}{\#\textit{ of frames in time period}}\right) \times 100.$$

As examples, during the 1-min period before the water turned on, the blink rate would be 59 blinks per minute if the bird blinked 57 times with the left eye and 61 times with the right eye, the blink duration would be 0.077 s if the bird's blinks each lasted (on average) 0.080 s in the left eye and 0.074 s in the right eye, the percentage of time the bird spent blinking would be 7.5% if the bird spent 7.40% of its time with its left eye blinking and 7.60% of its time with its right eye blinking,

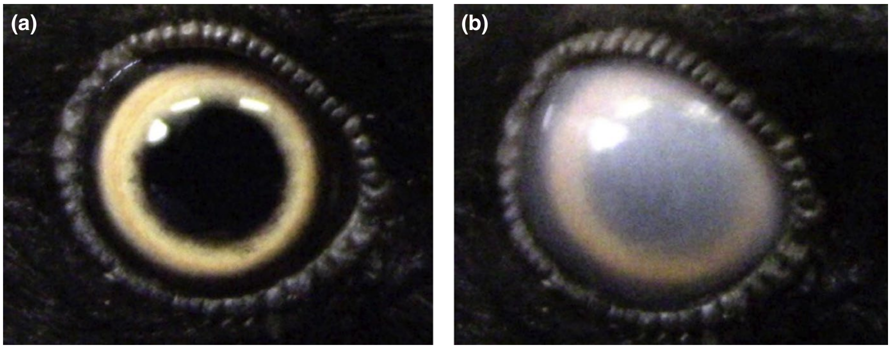

FIGURE 1 The right eye of a male great-tailed grackle when he is not blinking (a) and when he is blinking (b)

TABLE 1 The effect of treatment, time period, type, and their interaction as well as sex, order, temperature, and humidity on blinking behavior (composite factor including blink rate, blink duration, percentage of time spent blinking, and percentage of synchronized blinks). Statistically significant variables are indicated with an asterisk

	Numerator DF, denominator DF	*F*-value (*p*-value)
Overall model		
Treatment	1, 33	204.18 (<.001)*
Time period	2, 33	384.00 (<.001)*
Type	1, 33	5.57 (.024)*
Treatment*Time period*Type	7, 33	83.63 (<.001)*
Sex	1, 33	7.93 (.0081)*
Order	1, 33	0.06 (.81)
Temperature	1, 33	0.01 (.94)
Relative humidity	1, 33	0.06 (.81)
Comparisons		***t*-value (*p*-value)**
Head restrained		
Direct rain before versus. Indirect rain before	1, 33	1.27 (.21)
Direct rain during versus. Indirect rain during	1, 33	17.57 (<.001)*
Direct rain after versus. Indirect rain after	1, 33	4.93 (<.001)*
Head unrestrained		
Direct rain before versus. Indirect rain before	1, 33	0.69 (.49)
Direct rain during versus. Indirect rain during	1, 33	17.43 (<.001)*
Direct rain after versus. Indirect rain after	1, 33	4.50 (<.001)*
Indirect rain		
Before: Head restrained versus. Head unrestrained	1, 33	2.17 (.037)*
During: Head restrained versus. Head unrestrained	1, 33	2.10 (.043)
After: Head restrained versus. Head unrestrained	1, 33	1.11 (.27)
Direct rain		
Before: Head restrained versus. Head unrestrained	1, 33	1.69 (.10)
During: Head restrained versus. Head unrestrained	1, 33	1.51 (.14)
After: Head restrained versus. Head unrestrained	1, 33	1.42 (.17)

and the percentage of time they synchronized their blinks would be 93.2% if the bird's left and right eye were both blinking or both not blinking for 3,354 frames (out of the 3,600 frames). The mean values of the left and right eyes were used for blink rate, blink duration, and percentage of time the birds spent blinking because the blinking behavior in the left and right eyes was highly correlated (blink rate: $F_{1,35}$ = 1,037.75, $p < .001$; blink duration: $F_{1,35}$ = 1,153.5, $p < .001$; percentage of time the birds spent blinking: $F_{1,35}$ = 2,751.73, $p < .001$; linear mixed-effects models with repeated measures using the blinking behavior for the left eye as the dependent variable and for the right eyes as the independent variable).

2.5 | Statistical analysis

The data were analyzed using linear mixed-effects models with repeated measures in SAS (unstructured covariance structure; PROC MIXED; Version 9.4; SAS Institute Inc.). Because the blinking variables were highly correlated, a factor analysis (using principal components as the method of extraction) was performed on the blinking variables (blink rate, blink duration, percentage of time spent blinking, and percentage of synchronized blinks) to extract a single factor ("blinking behavior;" Minitab version 18.1; Minitab Inc.). This factor score (natural log transformed to meet underlying assumptions of normality) was used as the dependent variable. The independent variables were the treatment (direct rain or indirect rain), time period (before, during, or after the water was turned on), type (head restrained or head unrestrained), and their interaction as well as the sex of the bird, treatment order (direct rain or indirect rain first), ambient temperature (mean across each minute time period), and ambient relative humidity (mean across each minute time period). Bird identity (random factor) was included within the model to account for repeated measures. A priori contrasts were performed to compare the blinking behavior between treatments, time periods, and type; Exactly 12 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; Benjamini & Hochberg, 1995). This model was also rerun using the individual blinking variables—blink rate (natural log transformed), blink duration, and percentage of time spent blinking (natural log transformed)—as the dependent variables; a similar model was rerun using the percentage of synchronized blinks as the dependent variable (PROC GLIMMIX; Poisson distribution; SAS Institute, Inc.).

Lastly, another linear mixed-effects model with repeated measures was run to examine headshaking. The model was similar to that described above except that headshaking rate (number of headshakes per minute) was the dependent variable, type was not included as an independent variable (because only head-unrestrained trials were analyzed), and a variance component structure was used (the structure that resulted in the best model fit).

3 | RESULTS

A single factor derived from varimax rotation explained 67.2% of the variance in the blinking variables. Three of the blinking variables loaded positively (blink rate, blink duration, and percentage of time spent blinking), and one of the blinking variables loaded negatively (percentage of synchronized blinks) on a single factor. The factor score coefficients were highest for the percentage of time spent blinking (blink rate: 0.24; blink duration: 0.28; percentage of time spent blinking: 0.36; and percentage of synchronized blinks: −0.32); similarly, the proportion of variability explained by the factor (communality) was highest for the percentage of time spent blinking (blink rate: 0.42; blink duration: 0.57; percentage of time spent blinking: 0.94; and percentage of synchronized blinks: 0.75).

The birds altered their blinking behavior when exposed to rainy conditions ($F_{1,33} = 204.18$, $p < .001$; Table 1; Figure 2; Movie S1). Based on the composite blinking behavior variable, an increase in blinking behavior indicated that the blink rate, blink duration, and percentage of time spent blinking increased while the percentage of synchronized blinks decreased. The blinking behavior of the grackles was higher when they were directly exposed to rain (water falling atop them) compared with when they were indirectly exposed to rain (water falling at a distance from them; head restrained: $t_{1,33} = 17.57$, $p < .001$; head unrestrained: $t_{1,33} = 17.43$, $p < .001$). In fact, the longest blink in the grackles occurred during the direct rain and lasted over 14 s. Before they were exposed to the direct or indirect rain, there was no difference in their blinking behavior (head restrained: $t_{1,33} = 1.27$, $p = .21$; head unrestrained: $t_{1,33} = 0.69$, $p = .49$). After they were exposed to the direct rain or indirect rain, their blinking behavior was higher in response to the direct rain compared with the indirect rain treatment (head restrained: $t_{1,33} = 4.93$, $p < .001$; head unrestrained:

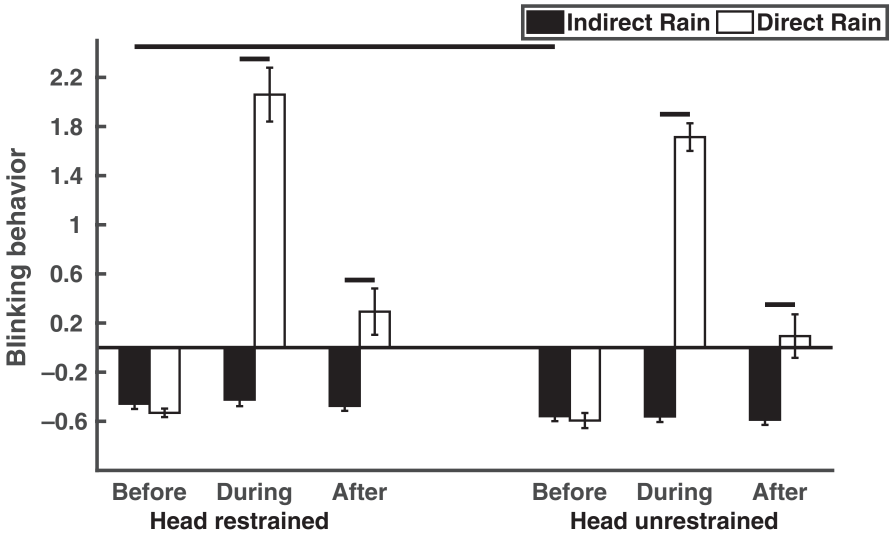

FIGURE 2 Blinking behavior (composite factor including blink rate, blink duration, percentage of time spent blinking, and percentage of synchronized blinks) before, during, and after the indirect rain or direct rain treatment ($n = 36$). Means and standard-error bars are shown; horizontal lines indicate planned comparisons that were statistically significant

$t_{1,33}$ = 4.50, $p < .001$). The birds' blinking behavior before, during, and after the indirect rain and direct rain was similar in the head-restrained and head-unrestrained trials (q* > 0.05) except they exhibited slightly elevated blinking behavior in the before period in head-restrained versus the head-unrestrained trials ($t_{1,33}$ = 2.17, p = .037). Overall, females exhibited increased blinking behavior compared with males (Table 1). The treatment order, ambient temperature (mean: 22.0°C; range: 19.2–27.1°C), and ambient relative humidity (mean: 76.5%; range: 52.7%–91.5%) did not impact blinking behavior ($p > .80$; Table 1). The results were qualitatively similar when the analysis was performed on the individual blinking variables (blink rate, blink duration, percentage of time spent blinking, and percentage of synchronized blinks; Table S1; Figures S1-S4).

The birds also exhibited headshaking during rainy conditions (Table 2). They exhibited higher rates of headshaking when they were directly exposed to rain (water falling atop them) compared with when they were indirectly exposed to rain (water falling at a distance from them; $t_{1,32}$ = 16.05, $p < .001$). In fact, they rarely exhibited headshaking (mean headshaking rate less than 1 shake/min) unless the water was falling directly atop them. When the water was falling directly atop them, their headshaking rate was relatively high (mean ± SE: 25.7 ± 2.6 shakes/min). Furthermore, they were blinking most of the time when they were exhibiting headshaking (mean percentage of time that they were blinking during headshaking: 92.4% ± 0.5%).

4 | DISCUSSION

Great-tailed grackles altered their blinking behavior when exposed to rainy conditions, supporting the hypothesis that rainfall influences blinking behavior. When they were directly exposed to simulated rainfall (water falling atop them), the grackles increased their blinking behavior compared with when they were indirectly exposed to simulated rainfall (water falling at a distance from them).

Because the nictitating membrane functions to protect and clean the eye surface (Sweeney et al., 2013), it is not surprising that grackles' blinking behavior increased under rainy conditions. The nictitating membrane can clear raindrops on the eyes that might otherwise obscure vision. In avian species that dive (e.g., ducks and loons), it has been suggested that the nictitating membrane remains continuously closed when these species are underwater to protect their eyes from the water (Ischreyt, 1914; Sivak, 1980). While the grackles did not continuously close their nictitating membrane during rainy conditions, the birds kept their nictitating membrane closed during a single blink for more time when experiencing direct rain versus indirect rain. Interestingly, females exhibited increased blinking behavior compared with males. Given that female eyes are smaller than male eyes (Johnson & Peer, 2001), it is possible that rain has stronger impacts on smaller versus larger eyes; if this is the case, species with smaller eyes might likewise be more impacted by rain versus species with larger eyes.

In addition, grackles' blinking behavior remained elevated even after the direct rain stopped, potentially because it took time for eye physiology to return to equilibrium (Quallo et al., 2015). After the direct rain stopped, very little water fell onto the birds' eyes (any remaining water droplets on the birds' heads quickly fell off). While no previous studies have examined the impact of rain on blinking behavior, our results are similar to those showing that ocular irritants increase blinking behavior in humans (Nakamori et al., 1997; Wu et al., 2014; Yang et al., 2001) and birds (Yorzinski & Argubright, 2019). Future studies could determine how blinking behavior is influenced by differing intensities of rain, ranging from light rain to torrential rain.

The blinking behavior of the grackles' left and right eyes was not always synchronized. The blinking behavior was synchronized the least during and after the rainy conditions. In an extreme case during direct rain, the bird's blinking behavior was synchronized only 36.6% of the time, with the bird spending 70.3% of her time blinking with the left eye but only 8.2% of her time blinking with the right eye; during this trial, the bird was oriented such that the water was falling heavily on her left but not right eye. This demonstrates that the birds can control their blinks independently in each eye and adjust them depending on the conditions.

TABLE 2 The effect of treatment, time period, and their interaction as well as sex, order, temperature, and humidity on headshaking. Statistically significant variables are indicated with an asterisk

	Numerator DF, denominator DF	*F*-value (*p*-value)
Overall model		
Treatment	1, 16	71.33 (<.001)*
Time period	2, 32	96.42 (<.001)*
Treatment*Time period	2, 32	97.41 (<.001)*
Sex	1, 15	0.28 (.60)
Order	1, 16	1.30 (.27)
Temperature	1, 77	0.03 (.86)
Relative humidity	1, 77	0.24 (.63)
Comparisons		***t*-value (*p*-value)**
Direct rain before versus. Indirect rain before	1, 32	0.34 (.74)
Direct rain during versus. Indirect rain during	1, 32	16.05 (<.001)*
Direct rain after versus. Indirect rain after	1, 32	0.50 (.62)

Head movements had minimal effects on the overall blinking behavior of grackles. Their blinking behavior was generally similar regardless of whether the birds' heads were restrained or not. Previous work has found that birds (Beauchamp, 2017; Yorzinski, 2016) and primates (Evinger et al., 1994; Gandhi, 2012) often blink when they move their heads, so it was possible that the grackles would have exhibited increased blinking behavior when their heads were unrestrained. However, the grackles did not necessarily exhibit many head movements even when their heads could move freely. Future studies that investigate the possible link between head movements and blinking behavior in grackles would be interesting given that head movements and blinking behavior are linked in many other species (Beauchamp, 2017; Evinger et al., 1994; Gandhi, 2012; Yorzinski, 2016).

When the grackles' heads were unrestrained, they often performed headshakes (rapid movements of their head from side to side) when they were directly exposed to the simulated rainfall. During these headshakes, they were often blinking. Similarly, Anna's hummingbirds (*Calypte anna*) also shake their heads under rainy conditions to expel water from their plumage (Ortega-Jimenez & Dudley, 2012). Additional studies could examine whether headshaking (either alone or in combination with blinking) facilitates enhanced vision during rainy conditions.

Due to their increased blinking behavior during rainy conditions, grackles likely experience significant impairments in visual processing. During blinks, their semi-transparent nictitating membranes sweep across the eyes and, therefore, likely limit visual input. In contrast, the nictitating membranes in many diving birds have a central transparent window (Ischreyt, 1914; Sivak, 1980) that may allow them to still see clearly even when their nictitating membranes are covering their eyes. Furthermore, blinks in grackles may completely block visual input by suppressing neural activity in areas of the brain associated with perceiving environmental change, a phenomenon that has been demonstrated in humans (Bristow et al., 2005; Volkemann et al., 1980) but has never been tested in birds. However, it is also possible that the grackles can compensate for any costs associated with blinking behavior using specialized neural processing abilities or performing behavioral adjustments. For example, when conditions are rainy, redshanks (*Tringa totanus*) forage in areas with low predation risk and harbor seals (*Phoca vitulina*) are highly vigilant (Granquist & Sigurjonsdottir, 2014; Hilton et al., 1999); it is possible that they are adjusting their behavior to compensate for impaired vision resulting from the rainy conditions. Assuming grackles have limited or no visual input during blinks, their increased blinking behavior during and after rainy conditions would likely lead to impaired visual processing that influences their behavioral abilities (such as predator detection and obstacle avoidance). In fact, some evidence suggests that birds are more likely to collide with obstacles (airplanes, wind turbines, and vessels) during rainy conditions (Gotoh, Takezawa, & Maeno, 2012; Manktelow, 2000; Merkel & Johansen, 2011; Osborn, Higgins, Usgaard, Dieter, & Neiger, 2000), potentially because their ability to visually detect these obstacles is limited. It is possible that many species limit activity during rainy conditions (Belwood & Fullard, 1984; Hume, 1986; Kennedy, 1970; Robbins, 1981; Sergio, 2003; Touchton et al., 2002), especially during heavy rain, to avoid possible costs associated with increased blinking; however, limiting their activity during rainy conditions might reduce the time they have to accomplish other behavioral goals.

Because abrupt weather will likely become more prevalent due to climate change (Easterling et al., 2000; Min, Zhang, Zwiers, & Hegerl, 2011), a greater understanding of its impact on sensory ecology will become increasingly important. While animals can modify their physiology and behavior in response to abrupt weather changes, we have a limited understanding of how they do so (Buchholz et al., 2019). Blinking behavior is a fundamental aspect of visual processing that is influenced by environmental conditions (Nakamori et al., 1997; Wu et al., 2014; Yang et al., 2001; Yorzinski & Argubright, 2019). Further studies that examine how weather impacts visual processing, including blinking, will help uncover how animals adjust to weather extremes.

ACKNOWLEDGMENTS

I thank Anna Alvarez, Ileana Moore, and Logan Wirth for scoring the blinking behavior from the videos. This work was supported by the College of Agriculture and Life Sciences at Texas A&M University and Texas A&M AgriLife Research.

CONFLICT OF INTEREST

The author declares that she has no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Yorzinski JL. Blinking behavior in great-tailed grackles (*Quiscalus mexicanus*) increases during simulated rainfall. *Ethology*. 2020;00:1–9. https://doi.org/10.1111/eth.13003