



U.S. Department of Agriculture
Animal and Plant Health Inspection Service
Wildlife Services

U.S. Government Publication



Effects of visual obstruction, prey resources, and satiety on bird use of simulated airport grasslands



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ARTICLE INFO

Article history:

Received 31 March 2016
Received in revised form 22 August 2016
Accepted 11 October 2016
Available online 19 October 2016

Keywords:

Airport grassland
Antipredator behaviour
Bird-aircraft collisions
Brown-headed cowbird
Molothrus ater
Perceived risk

ABSTRACT

Grasslands represent 39%–50% of U.S. airport properties, and a recent management framework recommended exploiting both antipredator behaviours and food resources in airport grasslands to curb use by birds considered hazardous to aviation safety. We evaluated framework predictions empirically by exposing unsated and sated brown-headed cowbirds (*Molothrus ater*) to visually obstructive (~13-cm vegetation height; tall), higher-risk plots versus unobstructive (<8 cm vegetation height; short) plots, and relative to prey resources. We predicted that 1) unsated birds (unfed since the previous day) would be present in greater numbers and forage more in short than tall vegetation plots 24 h post-mowing because of invertebrate flush resulting from mowing; 2) unsated birds would show increasing numbers and foraging in tall plots >24 h post-mowing because of decreasing food abundance and availability in short plots; and 3) sated birds would be present in greater numbers and forage more in short vegetation overall, because vigilance needs would exceed that of food needs. We evaluated effects of visual obstruction (a metric correlated with both vegetation height and insect density) on behaviours within plots via generalized linear mixed models. Unsated cowbirds showed nearly equal numbers in tall and short plots (\bar{X} [SE] individuals using tall plots: 9.5 [5.1]; short plots: 9.8 [5.1], $P=1.00$, Wilcoxon Signed Ranks Test), and foraged nearly equally in both plots 24 h post-mowing (tall plots: 6.9 [4.7] individuals; short plots: 6.6 [4.1] individuals, $P=0.94$). Prey availability was likely enhanced within short plots within 24 h of mowing, but possibly in adjacent tall plots as well. Over the course of the experiments (8–9 days) unsated cowbirds showed no difference in numbers between plots (tall plots: 8.2 [4.9] individuals; short plots: 11.4 [4.9] individuals, $P=0.13$), but foraged more in short plots (tall plots: 4.4 [3.8] individuals; short plots: 7.8 [4.2] individuals, $P=0.01$); visual obstruction was significantly and negatively correlated with foraging in tall plots. Sated cowbirds selected for short plots (use of tall plots: 5.9 [4.2] individuals; short plots: 11.7 [4.6] individuals, $P<0.01$; foraging in tall plots: 4.1 [3.3] individuals; short plots: 8.2 [4.6] individuals, $P<0.01$). Our findings support recommendations for use of visually obstructive vegetation in combination with proactive control of food resources to reduce use of airport grasslands by birds that select against visually obstructive cover.

Published by Elsevier B.V.

1. Introduction

Wildlife collisions with aircraft (strikes) represent a substantial safety and economic burden to civil aviation worldwide (Allan, 2002; DeVault et al., 2013; Anderson et al., 2015). Bird strikes composed 97% of strikes reported to the U.S. Federal Aviation Administration (FAA) from 1990–2014 (Dolbeer et al., 2015). Fur-

ther, approximately 72% of all bird strikes reported to the FAA occurred ≤ 152 m above ground level (AGL), thus within the airport environment; these strikes represented approximately U.S. \$640 million annually in direct and indirect costs to the civil aviation industry operating within the USA (Dolbeer et al., 2015; see also Anderson et al., 2015).

Given the predominance of strikes within the airport environment, management of wildlife and habitats that serve as resources to birds is a critical component of strike reduction (Blackwell et al., 2009a, 2013; Dolbeer, 2011; DeVault and Washburn, 2013). Grasslands, for example, represent 39% to 50% of U.S. airport properties (DeVault et al., 2012). Management of grasslands at U.S. airports,

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particularly, has focused more on vegetation height than a comprehensive examination of species use and associated foraging and antipredator behaviours (e.g., Blackwell et al., 2013 Supporting information 2, including citations therein; Washburn and Seamans, 2013). A recent management framework suggested exploiting both antipredator behaviours (via management of vegetation height) and food resources (via mowing and chemical controls) in airport grasslands to curb use by birds considered hazardous to aviation safety (Blackwell et al., 2013).

Specifically, Blackwell et al. (2013) theorized that with fluctuations over time in prey availability within an airport's vegetation community, habitat structure likely plays a key role in avian use of airport habitats by affecting not only prey availability, but perceived predation risk (e.g., Devereux et al., 2004; Whittingham and Devereux, 2008). Our purpose was to evaluate the framework predictions empirically by exposing brown-headed cowbirds (*Molothrus ater*) to visually obstructive (~13-cm vegetation height; tall), presumably higher-risk plots (e.g., Beauchamp, 2015), versus un-obstructive (<8 cm vegetation height; short) plots. Brown-headed cowbirds (hereafter, cowbirds) are omnivorous species known to selectively forage in less visually obstructive environments (Morris and Thompson, 1998; Shaffer et al., 2003; Seamans et al., 2007). However, cowbirds will also use visually obstructive habitats based on prey availability (e.g., Morris and Thompson, 1998). This adaptability to grassland structure and food resources makes this species useful to testing hypotheses directed toward ecologically based management of airport grasslands to deter use by obligate and facultative grassland bird species. In addition, within our study area cowbirds are easily captured during spring migration, fare well in captivity, and have served as a surrogate species in behavioural studies examining a variety of issues associated with small, flocking birds (e.g., Icteridae) involved in bird strikes (Seamans et al., 2007; Blackwell et al., 2009b; Doppler et al., 2015; DeVault et al., 2015). Also, cowbirds were involved in 1973 a strike that resulted in seven fatalities (Thorpe, 2003). Further, there have been 185 reports to the FAA (1990–2014) involving cowbirds struck by aircraft; 51 instances which involved multiple birds (Dolbeer et al., 2015).

We predicted that 1) food-deprived (hereafter unsated) birds would be present in greater numbers and forage more in mown vegetation plots 24 h post-mowing than in tall, visually-obstructive plots because of effects of invertebrate flush from recent mowing (see Blackwell et al., 2013); 2) unsated birds would show increasing numbers and foraging in tall plots >24-h post-mowing because of decreasing food abundance and availability in short plots (Blackwell et al., 2013 Supporting information 2; see also Peggie et al., 2011), indicative of more risk-prone behaviour; and 3) fed (hereafter sated) birds would be present in greater numbers and forage more in short vegetation as vigilance needs take on a greater importance over food needs through time. Our ultimate objective was to use our findings to better inform management of airport grasslands relative to deterring use by birds that select against visually obstructive vegetation.

2. Methods

2.1. Ethics statement

The study was conducted following approved National Wildlife Research Center Protocol, 2068.

2.2. Study area

We conducted our study on the 2200-ha National Aeronautics and Space Administration's (NASA) Plum Brook Station (PBS; Erie

County, OH, USA; 41° 22' N, 82° 41' W; see Bowles and Arrighi, 2004 for detailed description of PBS). Our experimental site consisted of approximately 900 m² of mixed turf grass and forbs. Approximately 25% of the area had been mown regularly during spring and summer for over two decades. We recovered the remainder from grass and shrub habitat during 2012, tilled the soil and sowed a mixture of cool-season grasses (e.g., *Poa pratensis*, *Festuca arundinacea*). The entire site was fertilized in 2012 and 2013 in preparation for our 2014 experiments.

2.3. Cowbird capture and maintenance

We captured 250 male cowbirds using decoy traps on PBS (April–May 2014). Captured birds were held in six 2.4- × 2.4- × 1.8-m cages containing ≥ 13.7 m of perch space/cage (maximum of 50 birds/cage) in an enclosed aviary with a concrete floor on PBS where they received a maintenance diet, and water ad libitum (National Wildlife Research Center, NWRC, Protocol 2068). Aviary windows were of wire mesh with only an awning enclosure, which was always open. Each end of the aviary was fitted with sliding doors that opened to approximately 90% of the width of the building; these doors were opened each day at approximately 0800 h and closed by 1600 h. Thus, all birds were exposed to the prevailing light-dark cycle and ambient temperature conditions. The birds were released upon completion of the study.

2.4. Experimental protocol

Behavioural research conducted using captive birds inherently imposes restrictions on inference to factors affecting particular behaviours (e.g., responses to predation risk). However, these caveats can be balanced, via sound experimental design, against the increased logistics and potentially inadequate data collection in natural settings where controls are minimal or nonexistent. With regard to avian foraging and antipredator behaviours, previous behavioural research was conducted primarily using relatively small (0.5 m³) enclosures (e.g., Devereux et al., 2004, 2006a,b,c, 2008). These smaller cages inhibit natural behaviours (e.g., flight), but are useful in testing questions requiring controls with regard to bird interactions, vegetation composition, and influence of specific predator stimuli. Here, however, we chose to allow our experimental groups (see Experimental protocol, below) to select vegetation conditions and respond to other group members, as well as visual and auditory stimuli from free-ranging wildlife near our study site.

We established ten 3.6- × 8.0-m flight cage locations (not separate flight cages) within our study site that were arranged in three columns, one comprising five locations, another with four locations, and a third with a single location based on levelness of the ground (Fig. 1). Each location consisted of two, 2.4- × 2.4-m vegetation plots, with 0.61-m buffers of vegetation that were maintained in the same manner as the respective plot. Flight cage locations within a column were separated by approximately 2.0 m.

We used a single flight cage (4.8- × 4.8- × 3.6 m or ~83 m³), designed such that each half could be moved to a new location independently, positioned over the plots and in contact with the other cage half. This design allowed us to expose each cowbird group to a unique location (Fig. 1). In addition, we positioned two closed-circuit digital cameras (Illustra Flex 800, American Dynamics, 6600 Congress Avenue, Boca Raton, Florida, USA 33487) mounted on tripods outside of the cage and at 90° to the opposing camera (Fig. 1). We used pre-measured lines that were secured to cage corners to position each camera at the same elevation and distance from each cage and the respective plots (i.e., insuring the same area of video coverage after the cage was repositioned in a new location). All lines were removed prior to data collection. Cabling for each camera ran to an observation trailer approximately 60 m from

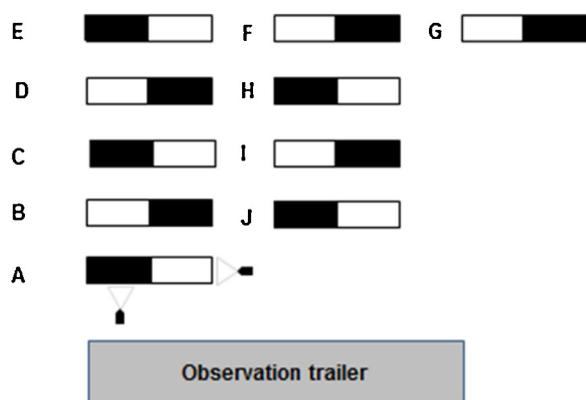


Fig. 1. Locations (larger rectangles) for experiments involving exposure of captive brown-headed cowbirds to visually obstructive (~13-cm vegetation height; smaller black rectangles) versus un-obstructive vegetation plots (<8 cm vegetation height; smaller white rectangles), and relative to prey resources and bird satiety. A single, easily moveable flight cage (4.8 × 4.8 × 3.6-m or ~83 m³) was moved to a new location (A–G) for each bird group tested. Camera locations are indicated in location A. Cameras were positioned in the same manner each time the cage was moved to a different location. The observation trailer was approximately 60 m from location A. Experiments were conducted in Erie County, Ohio, USA (41° 22' N, 82° 41' W) from 17 June through 22 July 2014. See text for further details on site conditions and cage placement methods.

location A (Fig. 1), where video was stored for review. Our use of two cameras and the movable cage allowed us to easily replicate across 10 locations per observation day.

We mowed all plots to approximately a 6.0-cm height, using a tractor-drawn mowing deck, 15 days prior to our first experiment; all plots were raked of cut swards. In location A (Fig. 1), we randomly selected a plot to serve as the short plot. For each consecutive location thereafter (i.e., B–J), we alternated between sides for the tall and short plots such that we controlled for potential bias associated with directionality and influences from outside the experimental site. However, because our approach entailed semi-natural conditions, our plots were exposed to natural movements of invertebrates as well as movements associated with mowing.

We began our first experiment, involving unsated cowbirds, on 17 June 2014 and conducted observations on 19 and 25 June as well. Our protocol involved the exposure of unsated, naïve cowbird groups (N = 30 groups, 4 birds/group, 10 groups/day, 3 observation days) to visually obstructive versus unobstructive vegetation and period since mowing. Cowbird groups were deprived of food since 1530 h on the previous day. We mowed plots designated as short plots to approximately 3 cm height on 16 June (24 h prior to the first observation) by using a standard push-mower with bag attachment to collect cut swards. Tall plots (originally mown on 2 June 2014) were not mown again (Table 1).

Mowing not only reduced visual obstruction within a plot, but as we noted above, affected the immediate and near-term movements of invertebrates within the plot and into surrounding unmown vegetation, including tall plots. However, these effects of invertebrate flush after mowing and subsequent invertebrate responses to vegetation, microclimate, and soil conditions are exemplary of the effects of grassland management at airports (Blackwell et al., 2013). To account for potential confounding effects, we quantified vegetation characteristics and invertebrate densities in both plots relative to period since mowing (see Plot vegetation and invertebrate sampling, below).

Because we used captive birds exposed briefly (i.e., during the experiment) to a greater perceived risk of predation, the likelihood for heightened levels of antipredator behaviour (e.g., scanning or use of visually un-obstructive habitat) was higher than what might be observed in natural conditions or periods of chronic exposure

Table 1

Contiguous, grass plots managed as either visually obstructive (~13-cm vegetation height, VH) or mown on day one to ~3 cm during avian use and foraging experiments conducted in Erie County, Ohio, USA (41° 22' N, 82° 41' W) from 17 June through 22 July 2014. Visual obstruction (VO) represents percent coverage of a 2.6 × 16-cm ruler, marked at 4-cm intervals, and held vertically within select plot area. Invertebrate density (ID) is presented as individuals/m². See text, Fig. 1, and Supplementary material Appendix A for details on plot design, and vegetation and invertebrate sampling.

Experiment	Tall Plot		Short Plot	
	Mean (SE)	Range	Mean (SE)	Range
Unsated cowbirds				
VH	11.6 (1.3)	8.0–14.0	5.3 (0.9)	3.0–7.5
VO	55.4 (14.1)	19.1–90.6	26.0 (5.6)	15.9–40.0
ID	169.7 (114.5)	51.5–544.1	69.8 (53.4)	4.4–164.7
Sated cowbirds				
VH	9.3 (1.9)	5.8–13.5	3.4 (0.8)	1.5–6.6
VO	46.5 (13.9)	24.3–76.9	14.6 (2.4)	10.1–19.3
ID	201.7 (81.2)	104.4–411.8	51.9 (24.8)	13.2–102.9

Table 2

Behavioural metrics scored for captive brown-headed cowbird use and foraging within contiguous, grass plots managed as either visually obstructive (~13 cm) or mown (~3 cm), during experiments conducted in Erie County, Ohio, USA (41° 22' N, 82° 41' W) from 17 June through 22 July 2014. See text for experiment details.

Behavioural Metric	Description
Foraging	An individual with head down below the horizontal plane of the body.
Vigilant	An individual with head up and neck extended for ≥5 s.
Other	An individual within a grass plot that is not foraging or overtly vigilant.

to predators (see Lima and Bednekoff, 1999). Therefore, we conducted two experiments, one using unsated birds to increase the possibility of risk-prone foraging relative to visual obstruction (e.g., Lima and Dill, 1990; Lima, 1998) and the other using sated birds. Groups were randomly selected (based on capture of the requisite 4 individuals/group from the main holding cages) and we conducted observations on only one group at a time. Subsequently, unsated groups were fasted from 18 to 22 h.

We introduced the first group of birds per day to either cage location A or J (Fig. 1) by 0935 h, with the cage location based on the completion of observations from the previous observation day. This later-morning release allowed time for evaporation of dew in the tall plot, a condition that might affect invertebrate activity and general plot use by birds (BFB, TWS personal observations). Each group was held in the enclosure for approximately 15 min. To allow for acclimation to the cage, we began data collection, based on video from the cameras, at minute seven. Specifically, at minute seven and thereafter at 2-min intervals through minute 15 (i.e., 5 data collection points) we quantified the number of birds using each plot. We also quantified the behaviours of birds per plot, as the number of individuals foraging, showing overt vigilance, or other behaviours within a respective plot (OTHER; Table 2). Devereux et al. (2004) classified active foraging by European starlings (*Sturnus vulgaris*) as when the head was lowered below the horizontal plane of the body and terminated when the head was raised above this plane for more than 5.6 s. However, because cowbirds have wide visual fields that allow information gathering while head down, as well as during head-up bouts (Fernández-Juricic et al., 2004a,b, 2005; Blackwell et al., 2009b), discerning vigilant behaviour is not necessarily clear-cut (Fernández-Juricic et al., 2005). Therefore, we opted for a measure of overt vigilance behaviour (Table 2).

To score behaviour at each interval we first reviewed video frames preceding and after the time for the measurement so as to locate each of the four birds (i.e., whether in the tall or short

plot, on the cage wall, or in flight). Foraging, vigilance, and other behaviours by birds in tall plots were at times difficult to discern because of obstruction by the vegetation. In those instances, we used the video frames bounding the time of measurement to look for movement of vegetation around the bird (i.e., indicating flushing of invertebrates) and evidence of overt vigilance in stationary individuals. When in doubt, we scored bird behaviour as OTHER. Here, we assumed that bias in determining foraging and vigilance behaviour for birds in tall plots might be revealed by significant and negative correlations with OTHER.

We conducted our second experiment, involving sated cowbirds, on 15, 17, and 22 July 2014 using the same protocol as outlined above, but with the exception that experimental groups were sated, exposed to food ad libitum prior to the experiment. We mowed short plots for this experiment on 14 July 2014.

2.5. Plot vegetation and invertebrate sampling

We sampled plot vegetation and invertebrates immediately after each day's observations. To estimate visual obstruction and vegetation height, we used a 20- × 50-cm frame (Daubenmire, 1959) at two randomly selected points (determined by blind toss of the frame) within the plot (see Fisher and Davis, 2010). Within the frame, we estimated the height of the vegetation, via 16-cm ruler, at or below the level which characterized 80% of the vegetation within the frame (i.e., the 80/20 height). In each corner of the frame (58 cm² per corner), we estimated an index of visual obstruction (see SM Appendix A for specific details on vegetation sampling).

We sampled invertebrates within each plot via vacuum sampling (SM Appendix A). There are inherent biases associated with invertebrate sampling that affect abundance and biomass estimates (Doxon et al., 2011; see also SM Appendix A). Therefore, we consider our samples as broad indices of invertebrate abundance within each plot type. Also, all plots were open to invertebrate movements. Thus, we sampled without replacement from an open population.

All invertebrate samples were individually sorted and all individuals found within each sample were identified via dissecting microscope to the lowest practical taxonomic level (via Triplehorn and Johnson, 2005), counted, and body length measured to the nearest millimeter. Most individuals were identified to family. But, in many cases we found only remnant body parts, a condition which compromised classification to lower taxonomic levels, as well as accurate estimation of the number and biomass of individuals of a particular taxon represented in the sample. Where possible, we recorded whether taxa were associated with the soil surface or foliar. We identified and classified individuals into functional feeding groups based on consensus information using Triplehorn and Johnson (2005), McAlpine et al. (1981, 1987), and Eaton and Kaufman (2007). We provide identification, general habitat, and raw counts for invertebrates in SM Table S1.

2.6. Statistical analyses

Because of the timing of the two experiments, and thus potential biases associated with natural movements by invertebrates and in response to the two mowings of the short plots, as well as ambient factors that can contribute to avian behaviour (e.g., temperature, wind), we conducted our analyses within experiment.

As stated above, invertebrate sampling provided an index for the overall productivity of the two plot types, considering bias in capture and condition of individuals, thus we did not differentiate between likely and unlikely invertebrate prey (see Morris and Thompson, 1998). We calculated the density of invertebrates per bird group and plot type by simply dividing the total number of individuals recovered across orders (SM Appendix A) by 0.68 m², the area sampled.

In preliminary analyses we found that both invertebrate density and vegetation height in tall plots were positively correlated with visual obstruction (Pearson Correlation Coefficient, experiment 1, unsated birds, density vs. visual obstruction: $r=0.64$, $|P|<0.01$; height vs. obstruction: $r=0.55$, $|P|<0.01$; experiment 2, sated birds, density vs. obstruction: $r=0.46$, $|P|=0.01$; height vs. obstruction: $r>0.84$, $|P|<0.01$). Therefore, we opted to exclude invertebrate density and vegetation height from our main analyses, but used visual obstruction instead. We examined the contribution of invertebrate density to our foraging model (below) in a post-hoc analysis. We report descriptive statistics for invertebrate density and vegetation height.

In addition, our observations within a cage location for an individual group were not independent (i.e., birds using one plot were not independent of those using the other plot) and not all birds were on the ground during each of the five observations per group. Therefore, in place of preference analyses for bird numbers and foraging by plot type, we conducted a Wilcoxon Signed Ranks test within experiment to examine the paired difference by group and plot relative to zero for bird numbers and foraging, respectively.

We modelled bird use of and foraging within tall and short plots, respectively, by using generalized linear mixed model analyses (PROC GLIMMIX, SAS 9.2, Cary, NC, USA). Our response variables for each group reflected the summed counts of birds for the respective variable across the five observations per plot made during the 15-min period. We modelled bird numbers in tall and short plots, respectively, relative to visual obstruction. We modelled foraging relative to visual obstruction and OTHER within the specific plot. As for vigilance, our observations were too few to assess relative to visual obstruction (see Results).

Based on non-normal distributions of our independent variables as well as model error, we modelled each response relative to a gamma distribution and using the Identity link. Because each cage location was used by three groups over the three observation days, we included an R-side, or residual random effect with flight cage location as the subject and an autoregressive correlation structure. The use of cage location as a random effect also allowed us to examine the potential effect of day of observation within location on use of and foraging behaviour within tall plots (hypothesis 2: unsated birds would show increasing numbers and foraging in tall plots >24-h post-mowing because of decreasing food abundance and availability in short plots).

We used residual log likelihood of the linearized model (i.e., Residual Pseudo-likelihood, Res. PL; PROC GLIMMIX, SAS 9.2, Cary, NC, USA) for parameter estimation. We examined each model for overdispersion via variance inflation factor, Generalized Chi-square/df. We examined differences in response variable by group and plot, as well as effects of independent variables at $\alpha=0.05$.

3. Results

Across experiments our observations of vigilant birds were rare (i.e., 2 instances across groups and plots over the 2 experiments; ~0.7% of all observations). Birds showing head-up behaviour >5 s were often relaxed with regard to neck extension, or head-up behaviour was associated with apparent attempts to find exit points in the cage netting. Clearly, some of these birds were watchful, but not vigilant by our definition (see above). Further, our cage allowed ample room for flight or perching on the netting, a position that also aided vigilance (see also Blackwell et al., 2009b).

Invertebrates sampled across our experiments were primarily foliar species (71%; SM Table S1). This finding is indicative of the potential bias associated with use of only a single sampling method for invertebrates. That said, our intent was to index potential invertebrate prey resources, not delineate these resources in

Table 3

Captive brown-headed cowbird use and foraging within contiguous, grass plots managed as either visually obstructive (~13 cm) or mown (~3 cm) during experiments conducted in Erie County, Ohio, USA (41° 22' N, 82° 41' W) from 17 June through 22 July 2014. Our design comprised the exposure of 30 groups, four birds per group, and 10 groups per day to the plot conditions in 10 separate locations. These data represent observations across groups. We conducted two experiments based on whether the birds were fed the night previous to the experiment (i.e., sated versus unsated experimental groups). Differences significant at $\alpha = 0.05$ are noted as *. See text for details on statistical analysis.

Experiment	24 h post mowing				Across Experiment			
	Tall Plot (individuals)		Short Plot (individuals)		Tall Plot (individuals)		Short Plot (individuals)	
	Mean (SE)	Range	Mean (SE)	Range	Mean (SE)	Range	Mean (SE)	Range
Unsated cowbirds-plot use	9.9 (5.1)	2–19	9.8 (5.1)	1–18	8.2 (4.9)	0–19	11.4 (4.9)	1–20
Unsated cowbirds-foraging	6.9 (4.7)	1–14	6.6 (4.1)	0–13	4.4 (3.8)	0–14	7.8 (4.2)*	0–16
Sated cowbirds-plot use	7.4 (4.1)	0–14	12.2 (4.4)	6–20	5.9 (4.2)	0–14	11.7 (4.6)*	0–16
Sated cowbirds-foraging	5.7 (3.2)	4–16	10.1 (4.6)	4–16	4.1 (3.3)	0–9	8.2 (4.6)*	0–16

detail relative to soil surface and foliar position. Further, in each experiment invertebrate density was either not a significant predictor of foraging ($P \geq 0.48$ for the parameter estimate per model), or model fit was not improved.

3.1. Experiment: unsated brown-headed cowbirds

Our experiment with unsated cowbirds comprised 28 groups because we were forced to remove ill or injured birds on the second observation day of the experiment. During this experiment, birds were exposed, on average, to 27.7 (SD=6.9) °C during observations, with groups 1–10 experiencing 32.2 °C. Wind conditions were generally below 12 km/h, with the exception of groups 1–10 which experienced gusts up to 29 km/h.

Over the nine days of this experiment, we achieved close approximation to our 13-cm, 80/20 vegetation height target for tall plots and 3-cm target height for short plots (Table 1). Mean visual obstruction in tall plots exceeded that of short plots by a factor of 2.1 (Table 1). Invertebrate density in tall plots exceeded that of short plots on average by a factor of 2.4 (Table 1).

3.2. Plot use by unsated cowbirds

We found no difference in mean bird number within plots for unsated cowbirds exposed to treatment 24 h after the mowing of the short plots ($S = 0.0$, $P = 1.00$; Table 3). Across the three observation days (i.e., across 28 groups), 49% of unsated cowbirds were, on average, observed in the plots. Numbers within short plots did not differ from that of tall plots, ($S = -64.0$, $P = 0.13$; Table 3).

The variance in our data relative to our models indicated no overdispersion (Table 4). Flight cage location (Table 4) exerted no effect on model variance for bird numbers in tall plots (2 Res. PL=59.16, $X^2 = 2.83$, $P = 0.09$), but the effect was negatively correlated (Table 4) and marginally significant (-2 Res. PL=41.09, $X^2 = 3.88$, $P = 0.05$) for bird use of short plots. In other words, over the duration of the experiment cage location was associated with a nonsignificant reduction in use of short plots. However, we found no contribution of visual obstruction (i.e., increased or decreased) to bird numbers within either plot (Table 4).

3.3. Foraging by unsated cowbirds

We also found no difference in mean foraging within plots for the first 10 groups of unsated cowbirds groups ($S = 1.0$, $P = 0.94$; Table 3). Across groups, on average 30% of unsated cowbirds were foraging during our observations, and these birds foraged more in short than tall plots ($S = -100.0$, $P = 0.01$; Table 3).

We observed no overdispersion of data for either model (Table 4). Flight cage location (Table 4) posed no effect on bird foraging in either plot (tall: 2 Res. PL=77.80, $X^2 = 0.08$, $P = 0.78$;

short: 2 Res. PL=56.73, $X^2 = 0.56$, $P = 0.45$). Birds using tall plots and recorded as showing OTHER slightly exceeded those birds showing the same behaviour in short plots (tall: $\bar{X} = 3.8$ individuals, SE=3.2 individuals, range=0–10 individuals; short: $\bar{X} = 3.4$ individuals, SE=2.8 individuals, range=0–12 individuals). However, OTHER exerted no effect on foraging behaviour in either plot type (Table 4). In contrast, visual obstruction was significantly and negatively correlated with foraging in tall plots, but exerted no effect on foraging in short plots.

3.4. Experiment: sated brown-headed cowbirds

During this experiment, birds were exposed to 22.7 (4.4) °C during observations. Our experiment with sated cowbirds involved 30 groups, spanned eight days, and we again achieved contrasting visually obstructive conditions for the respective plots (Table 1). Mean visual obstruction in tall plots exceeded that of short plots by a factor of 3.2 (Table 1). Also, invertebrate density in tall plots exceeded that of short plots on average by a factor of 3.9 (Table 1). Over the experiment, mean invertebrate density in tall and short plots decreased by factors of approximately 0.4.

3.5. Plot use by sated cowbirds

Despite counts favouring number of birds in short over tall plots by a factor of approximately 1.6, we found no difference in use by sated cowbirds 24 h post-mowing ($S = -11.5$, $P = 0.12$; Table 3). Across groups 44% of sated cowbirds were, on average, observed in the plots and present in greater numbers in short than tall plots ($S = -133.5$, $P < 0.01$; Table 3).

Our data were not overdispersed relative to either model of plot use (Table 4). Flight cage location (Table 4) exerted no effect on use in either plot type (tall: -2 Res. PL=73.02, $X^2 = 0.50$, $P = 0.48$; short: -2 Res. PL=36.92, $X^2 = 0.10$, $P = 0.75$). We found no contribution of visual obstruction to use of either plot type (Table 4).

3.6. Foraging by sated cowbirds

Within 24 h of mowing sated cowbirds foraged more in short plots than in tall plots by a factor 1.8, but paired comparisons were not different ($S = -10.0$, $P = 0.11$; Table 3). Over the experiment, on average 31% of sated cowbirds were foraging during the five observation times, and more so in short plots than in tall plots ($S = -100.5$, $P \leq 0.01$; Table 3).

Our data for both foraging models were not overdispersed (Table 4). Flight cage location (Table 4) was not a factor affecting foraging in either plot (tall: -2 Res. PL=86.51, $X^2 = 0.04$, $P = 0.84$; short: -2 Res. PL=58.28, $X^2 = 0.39$, $P = 0.53$). Birds using short plots and recorded as showing OTHER exceeded (by a factor of

Table 4
Results of generalized linear mixed model analyses of captive brown-headed cowbird numbers and foraging within contiguous grass plots managed as either visually obstructive (~13 cm) or mown (~3 cm) during experiments conducted in Erie County, Ohio, USA (41° 22' N, 82° 41' W) from 17 June through 22 July 2014. Our design comprised the exposure of 30 groups (however, see Results in text), four birds per group, and 10 groups per day to the plot conditions in 10 separate locations. We conducted two experiments based on whether the birds were fed the night previous to the experiment (i.e., sated versus unsated experimental groups). Response variables included 1) the number of birds present in the specified plot as a function of visual obstruction (use model); and 2) number of birds foraging in the specified plot as a function of visual obstruction and birds scored as in the plot but not foraging or vigilant (i.e., OTHER). We modeled each response relative to a gamma distribution using the Identity link. Because each cage location was used by three groups, we included an R-side, or residual random effect with site as the subject and an autoregressive correlation structure (AR1). We used Residual Pseudo-likelihood as the estimation technique. Covariance parameter (Cov Param) and independent variable estimates are shown as EST, respectively. Independent variable estimates significant at $\alpha = 0.05$ are noted as *.

Experiment-Resp. Var.	Cov Param	Est	SE	Var	Est	SE	DF	t	P	Gen. X ² /DF
Unsated birds- Use model (Tall plot)	AR(1)	-0.4718	0.2310	Intercept	2.3893	0.4101	9	5.83	0.0003	0.37
	Residual	0.3696	0.1190	Visual obst	-0.0054	0.0072	17	-0.74	0.4682	
Foraging model (Tall Plot)	AR(1)	0.0786	0.2753	Intercept	2.8648	0.6343	9	4.5	0.0015	0.66
	Residual	0.6556	0.1870	Visual obst	-0.0315	0.0112	16	-2.8	0.0122*	
				OTHER	0.0720	0.0489	16	1.5	0.1608	
Use model (Short plot)	AR(1)	-0.5000	0.2073	Intercept	2.3901	0.3876	9	6.17	0.0002	0.20
	Residual	0.1963	0.0635	Visual obst	0.0020	0.0149	17	0.13	0.8955	
Foraging model (Short Plot)	AR(1)	-0.2401	0.5500	Intercept	2.1110	0.5499	9	3.84	0.0040	0.31
	Residual	0.3079	0.0913	Visual obst	0.0021	0.0198	16	0.11	0.9164	
				OTHER	-0.0289	0.0377	16	-0.76	0.4555	
Sated birds- Use model (Tall plot)	AR(1)	0.1723	0.2411	Intercept	1.4967	0.4855	9	3.08	0.0131	0.52
	Residual	0.5239	0.1451	Visual obst	0.0058	0.0099	19	0.59	0.5641	
Foraging model (Tall Plot)	AR(1)	0.04814	0.2405	Intercept	0.9027	0.4993	9	1.52	0.1639	0.78
	Residual	0.7809	0.2141	Visual obst	0.0060	0.0102	18	0.51	0.6185	
				OTHER	0.1100	0.3498	18	1.25	0.2265	
Use model (Short plot)	AR(1)-cage loc	-0.0975	0.3094	Intercept	2.3470	0.4718	9	4.97	0.0008	0.16
	Residual	0.1616	0.0434	Visual obst	0.0078	0.0321	19	0.24	0.8095	
Foraging model (Short Plot)	AR(1)	0.1664	0.2567	Intercept	2.4551	0.6238	9	3.94	0.0034	0.30
	Residual	0.2994	0.0836	Visual obst	-0.01077	0.0408	18	-0.26	0.7946	
				OTHER	-0.06513	0.0272	18	-2.40	0.0275*	

1.9) those birds scored as OTHER in tall plots (tall: $\bar{X} = 1.8$ individuals, SE = 1.9 individuals, range = 0–8 individuals; short: $\bar{X} = 3.4$ individuals, SE = 3.6 individuals, range = 0–11 individuals). Neither increased visual obstruction nor OTHER affected foraging in tall plots, and visual obstruction exerted no effect on foraging in short plots (Table 4). However, foraging in short plots was, surprisingly, negatively correlated with OTHER (Table 4).

4. Discussion

Our prediction that use of short vegetation by small groups of unsated birds exposed to treatment 24 h post-mowing of those plots would exceed that of tall vegetation was not entirely upheld. Specifically, these first 10 groups of unsated cowbirds showed nearly equal numbers in tall and short plots. Similarly, unsated cowbirds foraged nearly equally in both plots 24 h post-mowing. Had the relatively extreme temperature and wind conditions on day one of the experiment involving unsated birds affected movements by the first ten groups, we consider that equal use and foraging between plots would have been unlikely. Instead, we suggest that the invertebrate flush associated with mowing likely enhanced abundance and availability in both adjoining plots, despite the fact that cowbirds tend to select for shorter vegetation (Morris and Thompson, 1998; Shaffer et al., 2003; Seamans et al., 2007).

The fact that cowbirds used and foraged equally in both plots has implications of bird deterrence within airport grasslands. Specifically, edge habitats created by inconsistent mowing or generally poor grassland maintenance at airports will inevitably contribute to increasing abundance of invertebrate prey (e.g., see Jacob and Brown, 2000; Dennis et al., 2001; Gardiner et al., 2002; Washburn and Seamans, 2013). In natural settings cowbirds will also use visu-

ally obstructive habitats based on prey availability (e.g., Morris and Thompson, 1998). In addition, cowbirds adapt to visually obstructive environments and perceived predation risk by adjusting scan rates relative to group size and neighbour distance (Fernández-Juricic et al., 2011). However, this adaptability to visually obstructive habitats does not connote that visual obstruction cannot be used in a management context. For example, we found that foraging by unsated birds in tall plots was negatively affected by visual obstruction. The implication is that managers must focus not simply on vegetation height, but also reduction in food resource availability and abundance.

We also predicted that unsated groups would show increasing risk-prone behaviour by their use of and foraging within tall plots >24-h post-mowing, assuming decreased food abundance and availability in short plots. Over the course of the experiment, we found no statistical difference in bird numbers between plots, but a negative correlation of cage location with use of short plots. In other words, there was a nonsignificant decline in use of the short plot over the experiment due to cage location.

In contrast to our prediction, however, we found significantly greater foraging by unsated cowbirds in short plots >24 h post-mowing. We recognize that the difficulty in discerning foraging behaviour for some birds in tall plots might have contributed to this difference, but our score for other behaviours (i.e., OTHER) in our foraging models was not significant. Again, invertebrate movements between plots or adjacent buffers might have sustained prey levels in short plots that were sufficient for foraging, with birds also benefitting by enhanced visibility of potential threats. For instance, we found that visual obstruction presented a significant, negative effect on unsated cowbird foraging in tall plots. That said, our finding of equal use (i.e., numbers of cowbirds) between plots >24 h post-mowing indicates that unsated cowbirds continued to sample tall vegetation.

With regard to sated birds, we found partial support for our prediction that these birds would show little risk-prone behaviour in use of tall plots. Specifically, we found no difference in numbers of sated cowbirds between plots 24 h post-mowing. As noted above, the invertebrate flush associated with mowing might have enhanced abundance and availability in both adjoining plots. However, over the experiment, numbers and foraging by sated cowbirds in short plots significantly exceeded that in tall plots. The negative correlation of sated cowbird foraging in short plots with OTHER indicates possible distraction of these birds away from foraging, but the underlying cause is unclear.

5. Conclusions

Small groups of unsated and sated brown-headed cowbirds exposed to variable prey resources and visually obstructive managed-grassland environments generally selected short vegetation for foraging, but also exploited visually obstructive vegetation. Our findings lend support to vegetation management regimens currently employed by the Civil Aviation Authority (CAA) in Great Britain and the Netherlands that prioritize visual obstruction and control of food resources (see Washburn and Seamans, 2013; and citations therein). However, such protocols should also be flexible relative to antipredator ecologies of any species using airport grasslands (e.g., those species that select for obstructive vegetation). Our findings with regard to periodic sampling of tall plots by brown-headed cowbirds, a species that selects for visually unobstructive vegetation, underscore the need to integrate management in an ecological context. Specifically, vegetation management to enhance visual obstruction and reduction of food resources within those habitats, integrated with other management (e.g., hazing), are key components to reducing use of airport grasslands by birds that select against visually obstructive environments.

Acknowledgements

Author salaries and research funding were provided by the U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center. We thank Brian Dorr, James Martin, Martin Stapanian, and Jeremy Wilson for comments on earlier versions of this manuscript.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.applanim.2016.10.005>.

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