



## Viewpoint

# A framework for managing airport grasslands and birds amidst conflicting priorities

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Management of modern airports is a task beset by conflicting priorities. Airports are vital to the global market economy, but impose costly environmental disturbances including habitat loss, noise, reduced air quality, erosion, introduction of invasive organisms, and polluted storm-water runoff (Blackwell *et al.* 2009). Airport environments also attract some wildlife hazardous to aviation safety, namely species involved in wildlife-aircraft collisions or 'strikes' (ICAO 2001, Blackwell *et al.* 2009, DeVault *et al.* 2011). Since 1912 at least 276 human lives have been lost due to bird strikes (Thorpe 2010), and from 1990 to 2010, more than 106 000 bird strikes involving civil aircraft were reported to the US Federal Aviation Administration (FAA; <http://wildlife-mitigation.tc.faa.gov/wildlife/>). Dolbeer (2006) reported that for strikes resulting in substantial aircraft damage (ICAO 1989), 66% occurred below 152 m altitude and within 1.5 km of a runway for airports servicing piston-powered aircraft only, and within 3 km of a runway for

airports servicing turbine-powered aircraft (FAA 2009). Consequently, aviation authorities prioritize human safety over wildlife conservation in management of airport habitats (ICAO 2001, FAA 2009).

Despite these problems, airports have been proposed as candidates for biodiversity conservation (Kelly & Allan 2006, Blackwell *et al.* 2009). For example, Kutschbach-Brohl *et al.* (2010) report that airport grasslands can provide habitat for a range of arthropod communities (e.g. Lepidoptera), and suggest the possibility of conserving these communities while minimizing provision of prey resources to birds recognized as hazardous to aviation. Moreover, declines in grassland bird populations in Europe and North America due to agricultural intensification and development have focused attention on enhancing quality and quantity of remnant grasslands (Herkert 1994, Vickery *et al.* 2004), including airport grasslands. In North America, airport properties have been identified as key areas of remnant grasslands important to obligate grassland bird species; species that both nest and forage in grasslands (Vickery *et al.* 1994, Askins *et al.* 2007).

Airport properties in the contiguous USA include > 330 000 ha of grassland, mostly annually mown areas, constituting 39–50% of airport property (DeVault *et al.* 2012). However, there is little research specific to airport environments that considers food resources for birds (Bernhardt *et al.* 2010, Kutschbach-Brohl *et al.* 2010), how birds perceive and react to predation risk (Baker & Brooks 1981) or disturbance (Kershner & Bollinger 1996), and no adequate assessment of how grassland management might affect strike risk (Blackwell *et al.* 2009, Martin *et al.* 2011).

In this context, we contend that promoting conservation of obligate grassland birds and managing to reduce bird hazards to aviation safety combines two potentially conflicting objectives in a single management framework. Ecologically based guidance to solve this potential conflict is limited, if not oversimplified. Here, we question the potential use of airports to conserve grassland birds, and assess the challenges in managing airport grasslands in light of current ecological and behavioural frameworks. We consider conditions for conservation of obligate grassland birds on airports, and evidence on the use of airports by frequently struck, grassland birds (both obligate and facultative). We also provide a framework to manage grassland birds at airports, given current information and uncertainty. Because of the availability of strike data via the FAA, our focus is on North America. However, problems associated with bird use of airport grasslands are international (ICAO 2001). Therefore, our ultimate purpose is better to inform current management, but also identify research gaps and establish specific predictions that will guide future studies on the ecological basis of use of airport grasslands by birds.

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## CONSERVATION POTENTIAL OF AIRPORT GRASSLANDS

Obligate grassland birds, particularly North American species, have declined markedly in distribution and abundance because of large-scale habitat loss and altered disturbance regimes (Askins *et al.* 2007). Airport grasslands offer potential habitat for the conservation of these species (Vickery *et al.* 1994, Askins *et al.* 2007), and a common objective of recent management and restoration efforts is to promote use by bird species exhibiting population declines (e.g. Rahman *et al.* 2011). However, despite an average of 113 ha of grassland per US airport (DeVault *et al.* 2012), these areas are typically non-contiguous, and the few patches of unmown or infrequently mown airport grassland are typically too small to support viable populations of obligate grassland species (e.g. Ribic *et al.* 2009). Nonetheless, some species, including Dickcissel *Spiza americana*, Eastern Meadowlark *Sturnella magna* and Bobolink *Dolichonyx oryzivorus*, have adequate fecundity in small isolated patches of disturbed grassland (e.g. Stauffer *et al.* 2011, Walk *et al.* 2011, Weidman & Litvaitis 2011).

Grassland management is as critical as patch size. Most grassland species require mature, unmanaged or infrequently managed grasslands during part of their life cycle (Askins *et al.* 2007), which generally harbour greater invertebrate and vertebrate species diversity and richness (Jacob & Brown 2000, Dennis *et al.* 2001, Gardiner *et al.* 2002). Ecological traps (Battin 2004) on airports are therefore possible when infrequently managed grassland areas are mown during the breeding season (Kershner & Bollinger 1996), although impacts on grassland species of conservation concern may be limited by adjusting timing of mowing relative to a species' breeding season (Brennan & Kuvlesky 2005).

## POTENTIAL CONFLICTS WITH AVIATION SAFETY

Irrespective of the conservation opportunities afforded by airport grasslands, problems remain with the attraction of species known to pose strike hazards to aviation (Martin *et al.* 2011). Separation of niches between grassland birds recognized as hazardous and non-hazardous to aviation, although a question of degree, is untenable, because providing high-quality, permanent habitat for grassland birds will conflict with the periodic alteration of vegetation structure necessary to reduce food and roosting resources used by species hazardous to aviation. As an example, mature grasslands may increase small mammal prey abundance for raptors, which are recognized as hazardous to aviation (Baker & Brooks 1981, Sodhi 2002, DeVault *et al.* 2011).

Given the limited conditions that would allow protection of grassland birds, use of airports as conservation areas would be restricted to locations outside zones designated for aircraft movements (FAA 2009). This restriction makes implementation of conservation measures for grassland birds both airport-specific and rare, as few airports manage large, contiguous grasslands beyond areas designated for aircraft manoeuvring. We contend, therefore, that conservation of obligate grassland birds on most airports without benefiting hazardous species appears unrealistic.

## AIRPORT GRASSLAND USE BY FREQUENTLY STRUCK SPECIES

Effective management of airport grasslands to prevent bird strikes should include an understanding of how species most hazardous to aviation use grasslands. Despite biases associated with the FAA National Wildlife Strike Database (e.g. reporting rate and species identification; DeVault *et al.* 2011), this is arguably the most complete set of long-term strike data available to the public. We compiled strike data for bird species involved in  $\geq 50$  strikes reported to the FAA (1990–2008) and found that species involved in the most damaging strikes use grasslands primarily for foraging rather than breeding (Supporting Information Table S1). Furthermore, these species generally select managed turf over mature grasslands (Supporting Information Data S1). Notably, 25 (47%) of the species identified in the analysis are infrequent users of grasslands and 11 (21%) are obligate grassland species, but only one of these is of conservation concern (Table S1).

Should airport grasslands therefore be managed to reduce use by species that cause the most damaging strikes, or would doing so accomplish little except trading one set of hazardous species for another? We suggest that any consideration of changes to management of airport grasslands be preceded by an examination of strike data (e.g. the FAA Wildlife Strike Database, <http://wildlife-mitigation.tc.faa.gov/wildlife/>). The assessment should focus on frequencies of associated damage, not just numbers of strikes (DeVault *et al.* 2011). Secondly, we suggest integrating strike data with an understanding of species' behavioural ecology, particularly foraging ecology and anti-predator behaviour (Supporting Information Data S2), because food availability and perceived predation risk play important roles driving selection of foraging habitats by grassland birds (Data S2), and can be managed locally by airport biologists. This two-tiered approach to management decision-making can then reduce strike risk by manipulating the foraging opportunities and perception of predation risk of those species most likely to cause damaging strikes.

### A MANAGEMENT FRAMEWORK

We propose a framework to manage airport grasslands to reduce bird strike risk by providing simplified scenarios targeting single species. We recognize that an airport biologist will need to manage more than one species simultaneously, but our framework can be used as a conceptual predictive tool to determine best management practices for species with the highest frequency of damaging strikes at a given airport. Also, because of our concerns regarding potential conflicts with conservation of grassland birds on airports and aviation safety, our framework does not include conservation scenarios.

We consider two seasonal scenarios with four conditional perspectives each, defined by whether a species perceives 13-cm-high grasslands as protective or obstructive during foraging, and whether food availability for that species is high or low (Fig. 1). First, assume that bird use of airport grasslands is represented by relatively small flocks or individual birds, characteristic of

spring migration and the breeding period. If a species perceives grassland as protective cover, we predict that it is more likely to use the airport when food availability is high (Data S2), as the grassland is perceived as a safe and food-rich micro-habitat. Under these conditions, we suggest mowing to enhance perceived risk and supplementing with wildlife-control measures to repel the species (Fig. 1). We predict that this same species will consider airport grasslands with protective cover but low food availability as unattractive. Under these conditions, only wildlife-control measures may be necessary (Fig. 1).

If a species perceives the grassland as obstructive cover (Data S2), its use might be limited to situations with high food availability. Thus, we suggest reducing food availability to create a high-risk and low-profitability patch, management of which can be supplemented by directed wildlife control (Fig. 1). Again, only directed wildlife control may be necessary in conditions of low food availability (Fig. 1).

		Food availability	
		Low	High
Small flocks/individual birds (e.g., spring migration):	Protective (not nesting)	(1) Maintain grass height (2) Directed wildlife control <sup>a</sup>	(1) Mow grass <sup>b</sup> (2) Directed wildlife control <sup>a</sup>
	Obstructive (head-down or head-up)	(1) Maintain grass height (2) Directed wildlife control <sup>a</sup>	(1) Reduce food availability • Insecticides <sup>c</sup> • Lumbricides <sup>c</sup> • Fertilizer <sup>d</sup> • Composition <sup>e</sup> (2) Directed wildlife control <sup>a</sup>
Large flocks (e.g., late summer and autumn migration):	Protective	(1) Mow grass <sup>b</sup> (2) Directed wildlife control <sup>a</sup>	(1) Mow grass <sup>b</sup> (2) Directed wildlife control <sup>a</sup>
	Obstructive (head-down or head-up)	(1) Maintain grass height (2) Directed wildlife control <sup>a</sup>	(1) Reduce food availability • Insecticides <sup>c</sup> • Lumbricides <sup>c</sup> • Fertilizer <sup>d</sup> • Composition <sup>e</sup> (2) Directed wildlife control <sup>a</sup>

**Figure 1.** A framework for management of airport grasslands to reduce use by avian species recognized as hazardous to aviation safety. Data relating airport grassland management to species-specific use, as well as strike rates, were unavailable. We therefore consider two scenarios and four conditional perspectives, and assume for each scenario a grassland that is 13 cm in height. Small species are those whose eyes are below 13 cm, large species those whose eyes are above 13 cm. Within each cell, we provide predictions (or management recommendations) as to how to reduce bird numbers in airfields for each combination of ecological conditions (food availability for a given species) and perception of risk in grasslands (providing protective or obstructive cover). Our predictions contrast with current airport grassland-management approaches in North America and Europe, which fail to consider the interaction of cover and food resources as affecting species behaviour. <sup>a</sup>Includes non-lethal harassment with regard to site and air-traffic conditions, as well as lethal control of the bird where necessary and permissible. <sup>b</sup>Mowing operations can be timed to reduce opportunity for bird responses to potential short-term pulses in availability of invertebrates. <sup>c</sup>Insecticide and lumbricide regulations vary by nation. <sup>d</sup>Fertilizer will enhance root structure and grass density, reducing food availability for probing species. <sup>e</sup>Grass composition (e.g. turf varieties) can be selected to reduce nutrition and palatability to grazing birds (e.g. Washburn & Seamans 2012).

In contrast, airport grasslands can experience frequent use by large foraging flocks during late summer and autumn, due to influxes of recently fledged young and migrating birds. As a result, this pulse in bird use of airports in North America is marked by increased strikes (<http://wildlife-mitigation.tc.faa.gov/wildlife/>). Furthermore, pressure of large numbers of foraging birds and variable resource availability could drive sampling of less than desirable habitats from food and cover perspectives, as noted for Common Starlings *Sturnus vulgaris* (Fernández-Juricic *et al.* 2004). From the perspective of species that perceive cover as visually obstructive, our predictions do not change (Fig. 1). However, if a species perceives cover as protective, we predict that enhancing perceived risk via mowing and supplementing with wildlife-control measures will reduce use (Fig. 1).

These predictions apply to both species whose vision in a vigilant body posture (head-up) is obstructed by the standard grassland height (eyes below 13 cm) or not (eyes above 13 cm). As examples, consider management of airport grasslands to reduce use by two frequently struck species, the Common Starling, a small, omnivorous probing forager, and the Canada Goose *Branta canadensis*, a large grazer (<http://wildlife-mitigation.tc.faa.gov/wildlife/>).

Starlings perceive taller vegetation as visually obstructive. Specifically, we associate the head-down position with foraging and some monitoring for predators, and the head-up position with monitoring only. Thus, grasslands  $\geq 13$  cm in height might reduce use by Starlings by increasing search times and time spent vigilant (Devereux *et al.* 2004, Whittingham & Devereux 2008). If, however, the availability of soil invertebrates is high near and on the soil surface, the benefits of food availability could outweigh perceived risk. Slower flock reaction times and less flock cohesiveness for Starlings foraging in food-rich patches with grass heights  $> 13$  cm (e.g. Devereux *et al.* 2008) could enhance strike risk upon disturbance (e.g. by increasing exposure time to approaching aircraft by responding starlings). Therefore, we recommend maintaining grass height, but reducing food availability via fertilizers, insecticides and lumbricides (as allowed) in combination with wildlife-control techniques (Fig. 1). For Canada Geese, airport grasslands maintained at 13 cm would be visually obstructive to the animal only when head-down (Fernández-Juricic *et al.* 2011). If Canada Geese use grasslands primarily for foraging (i.e. as opposed to loafing), we recommend a reduction in resource availability by changing grass composition to varieties that reduce nutrition and palatability (Washburn & Seamans 2012), in combination with wildlife-control techniques to reduce use (Fig. 1).

These recommendations can be considered 'static' in the sense that they do not take into consideration day-to-day changes in food availability and perceived predation risk. For instance, airport grasslands are generally

subject to mowing regimes to maintain a specified grass height, which in the short term after mowing might attract opportunistic species to exposed invertebrates (Peggie *et al.* 2011). Such an increase in bird numbers can translate into short-term increases in the risk of bird strikes but this effect can be countered by mowing at night in combination with enhanced wildlife control efforts (Fig. 1).

## CONCLUSIONS

We contend that conservation of obligate grassland birds on airport grasslands would conflict with aviation safety for most airports. Our framework integrates management of food and cover resources with foraging and anti-predator strategies of target species recognized as hazardous to aviation safety, as well as anticipated behavioural responses to disturbance. As such, effective use of our framework is contingent upon the integration of strike data with survey data of bird use of airport grasslands. Future research should empirically test predictions from our framework with the intention of incorporating the effects of seasonal influxes of bird populations to airport grasslands, and relative to management regimes, as well as short-term changes in vegetation structure, which can alter avian use and bird strike risk.

## REFERENCES

- Askins, R.A., Chávez-Ramírez, F., Dale, B.C., Haas, C.A., Herkert, J.R., Knopf, F.L. & Vickery, P.D. 2007. Conservation of grassland birds in North America: understanding ecological processes in different regions. Report of the American Ornithologists' Union Committee on Conservation. *Ornithol. Monogr.* **64**: 1–46.
- Baker, J.A. & Brooks, R.J. 1981. Distribution patterns of raptors in relation to density of meadow voles. *Condor* **83**: 42–47.
- Battin, J. 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conserv. Biol.* **18**: 1482–1491.
- Bernhardt, G.E., Kutschbach-Brohl, L., Washburn, B.E., Chipman, R.B. & Francoeur, L.C. 2010. Temporal variation in terrestrial invertebrate consumption by laughing gulls in New York. *Am. Midl. Nat.* **163**: 442–454.
- Blackwell, B.F., DeVault, T.L., Fernández-Juricic, E. & Dolbeer, R.A. 2009. Wildlife collisions with aircraft: a missing component of land-use planning on and near airports? *Landsc. Urban Plan.* **93**: 1–9.
- Brennan, L.A. & Kuvlesky, W.P. 2005. North American grassland birds: an unfolding conservation crisis? *J. Wildl. Manage.* **69**: 1–13.
- Dennis, P., Young, M.R. & Bentley, C. 2001. The effects of varied grazing management on epigeal spiders, harvestman and pseudoscorpions of *Nardus stricta* grassland in upland Scotland. *Agric. Ecosyst. Environ.* **86**: 39–57.
- DeVault, T.L., Belant, J.L., Blackwell, B.F. & Seamans, T.W. 2011. Interspecific variation in wildlife hazards to aircraft:

- implications for airport wildlife management. *Wildl. Soc. Bull.* **35**: 394–402.
- DeVault, T.L., Belant, J.L., Blackwell, B.F., Martin, J.A., Schmidt, J.A. & Burger, L.W. Jr** 2012. Airports offer unrealized potential for alternative energy production. *Environ. Manage.* **49**: 517–522.
- Devereux, C.L., McKeever, C.U., Benton, T.G. & Whittingham, M.J.** 2004. The effect of sward height and drainage on Common Starlings *Sturnus vulgaris* and Northern Lapwings *Vanellus vanellus* foraging in grassland habitats. *Ibis* **146**: 115–122.
- Devereux, C.L., Fernández-Juricic, E., Krebs, J.E. & Whittingham, M.J.** 2008. Habitat affects escape behaviour and alarm calling in Common Starlings *Sturnus vulgaris*. *Ibis* **150**: 191–198.
- Dolbeer, R.A.** 2006. Height distribution of birds as recorded by collisions with civil aircraft. *J. Wildl. Manage.* **70**: 1345–1350.
- Federal Aviation Administration (FAA).** 2009. Hazardous wildlife attractants on or near airports. Advisory Circular, AC 150/5200-33B. Airport Safety and Operations Division AA2-300.
- Fernández-Juricic, E., Siller, S. & Kacelnik, A.** 2004. Flock density, social foraging, and scanning: an experiment with starlings. *Behav. Ecol.* **15**: 371–379.
- Fernández-Juricic, E., Moore, B., Doppler, M., Freeman, J., Blackwell, B.F., Lima, S.L. & DeVault, T.L.** 2011. Testing the terrain hypothesis: Canada Geese see their world laterally and obliquely. *Brain Behav. Evol.* **77**: 147–158.
- Gardiner, T., Pye, M., Field, R. & Hill, J.** 2002. The influence of sward height and vegetation composition in determining the habitat preferences of three *Chorthippus* species (Orthoptera: Acrididae) in Chelmsford, Essex, UK. *J. Orthoptera. Res.* **11**: 207–213.
- Herkert, J.R.** 1994. The effects of habitat fragmentation on Midwestern grassland bird communities. *Ecol. Appl.* **4**: 461–471.
- International Civil Aviation Organization (ICAO).** 1989. *Manual on the ICAO Bird Strike Information System*. Doc 9332-AN/909. Montréal, Quebec, Canada.
- International Civil Aviation Organization (ICAO).** 2001. Air Navigation Commission, ANC Task No. AGA-0101: Bird strike and wildlife hazard reduction on or in the vicinity of airports. Preliminary review of a proposal for amendment to Annex 14, Volume 1. AN-WP/7672.
- Jacob, J. & Brown, J.S.** 2000. Microhabitat use, giving-up densities and temporal activity as short- and long-term anti-predator behaviours in common voles. *Oikos* **91**: 131–138.
- Kelly, T.C. & Allan, J.** 2006. Ecological effects of aviation. In Davenport, J. & Davenport, J.L. (eds) *The Ecology of Transportation: Managing Mobility for the Environment*. 5–24. New York: Springer.
- Kershner, E.L. & Bollinger, E.K.** 1996. Reproductive success of grassland birds at east-central Illinois airports. *Am. Midl. Nat.* **136**: 358–366.
- Kutschbach-Brohl, L., Washburn, B.E., Bernhardt, G.E., Chipman, R.B. & Francoeur, L.C.** 2010. Arthropods of a semi-natural grassland in an urban environment: the John F Kennedy International Airport, New York. *J. Insect Conserv.* **14**: 347–358.
- Martin, J.A., Belant, J.L., DeVault, T.L., Burger, L.W., Jr, Blackwell, B.F., Riffell, S.K. & Wang, G.** 2011. Wildlife risk to aviation: a multi-scale issue requires a multi-scale solution. *Hum.-Wildl. Interact.* **5**: 198–203.
- Peggie, C.T., Garratt, C.M. & Whittingham, M.J.** 2011. Creating ephemeral resources: how long do the beneficial effects of grass cutting last for farmland birds? *Bird Study* **58**: 390–398.
- Rahman, M.L., Tarrant, S., McCollin, D. & Ollerton, J.** 2011. The conservation value of restored landfill sites in East Midlands, UK for supporting bird communities. *Biodivers. Conserv.* **20**: 1879–1893.
- Ribic, C.A., Koford, R.R., Herkert, J.R., Johnson, D.H., Niemuth, N.D., Naugle, D.E., Bakker, K.K., Sample, D.W. & Renfrew, R.B.** 2009. Area sensitivity in North American grassland birds: patterns and processes. *Auk* **126**: 233–244.
- Sodhi, N.** 2002. Competition in the air: birds versus aircraft. *Auk* **119**: 587–595.
- Stauffer, G.E., Diefenbach, D.R., Marshall, M.R. & Brauning, D.W.** 2011. Nest success of grassland sparrows on reclaimed surface mines. *J. Wildl. Manage.* **75**: 548–557.
- Thorpe, J.** 2010. Update on fatalities and destroyed civil aircraft due to bird strikes with appendix for 2008 & 2009. 29th International Bird Strike Committee, Cairns (Australia). IBCS 29/WP.
- Vickery, P.D., Hunter, M.L., Jr & Melvin, S.E.** 1994. Effects of habitat area on the distribution of grassland birds in Maine. *Conserv. Biol.* **8**: 1087–1097.
- Vickery, J.A., Bradbury, R.B., Henderson, I.G., Eaton, M.A. & Grice, P.V.** 2004. The role of agri-environment schemes and farm management practices in reversing the decline of farmland birds in England. *Biol. Conserv.* **119**: 19–39.
- Walk, J.W., Kershner, E.L., Benson, T.J. & Warner, R.E.** 2011. Nesting success of grassland birds in small patches in an agricultural landscape. *Auk* **127**: 328–334.
- Washburn, B.E. & Seamans, T.W.** 2012. Foraging preferences of Canada Geese among turfgrasses: Implications for reducing human–goose conflicts. *J. Wildl. Manage.* **76**: 600–607.
- Weidman, T. & Litvaitis, J.A.** 2011. Are small habitat patches useful for grassland bird conservation? *Northeast. Nat.* **18**: 207–216.
- Whittingham, M.J. & Devereux, C.L.** 2008. Changing grass height alters foraging site selection by wintering farmland birds. *Basic Appl. Ecol.* **9**: 779–788.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Bird–aircraft collision (i.e. strike) data for avian species involved in at least 50 total strikes (with US civil aircraft or foreign, civil aircraft in the USA or its territories) reported to the FAA (1990–2008; summarized in the FAA Wildlife Strike Database; <http://wildlife-mitigation.tc.faa.gov/wildlife/>)<sup>a</sup>.

**Data S1.** Theoretical and empirical evidence