Canadian Journal of Zoology

Livestock grazing effects on flocks of seed-eating birds in the central Monte desert

Journal:	<i>Canadian Journal of Zoology</i>
Manuscript ID	cjz-2018-0223.R1
Manuscript Type:	Article
Date Submitted by the Author:	06-Jan-2019
Complete List of Authors:	Zarco, Agustin; Instituto Argentino de Investigaciones de las Zonas Áridas, Cueto, Víctor; Ecodes, CIEMEP, CONICET & UN Patagonia Sagario, M.Cecilia; Ecodes, Instituto de Investigaciones en Biodiversidad y Medioambiente (INIBIOMA – CONICET and UNComahue), Centro de Ecología Aplicada del Neuquén (CEAN), Junín de los Andes, Neuquén, Argentina. mctatysagario@gmail.com Marone, Luis; . Ecodes, Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA – CONICET). Mendoza, Mendoza, Argentina and Facultad de Ciencias Exactas y Naturales, UNCuyo. Mendoza, Mendoza, Argentina.
Is your manuscript invited for consideration in a Special Issue?:	Not applicable (regular submission)
Keyword:	Winter desert flocks, Grazed woodland, Flock structure, Nuclear species, Seed-eating birds

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A. Zarco, V.R. Cueto, M.C. Sagario, and L. Marone

A. Zarco. Ecodes, Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA), CONICET and Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Cuyo. Mendoza, Mendoza, Argentina. agustinzar@gmail.com

V.R. Cueto Ecodes, Centro de Investigación Esquel de Montaña y Estepa Patagónica (CIEMEP), CONICET and Universidad Nacional de la Patagonia San Juan Bosco. Esquel, Chubut, Argentina. vcueto@conicet.gov.ar

M.C. Sagario. Ecodes, Instituto de Investigaciones en Biodiversidad y Medioambiente (INIBIOMA), CONICET and Universidad Nacional del Comahue. Centro de Ecología Aplicada del Neuquén (CEAN). Junín de los Andes, Neuquén, Argentina. mctatysagario@gmail.com

L. Marone. Ecodes, Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA), CONICET and Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Cuyo. Mendoza, Mendoza, Argentina. lmalone@mendoza-conicet.gob.ar

Corresponding author:

V.R. Cueto. CIEMEP, CONICET and Universidad Nacional de la Patagonia. Esquel, Chubut, Argentina. (e.mail: vcueto@conicet.gov.ar)

A. Zarco. Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Cuyo. Mendoza, Mendoza, Argentina. +5492616655883 (e.mail: agustinzar@gmail.com)

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Abstract

Animal populations often decline due to habitat disturbance, but the initial response of organisms to human induced environmental change is usually behavioral. Intra- and inter-specific interactions can restrict or facilitate access to resources, resulting in changes to individual fitness, and resource depletion may affect the frequency and strength of interactions. In birds, it is often assumed that feeding in groups increases foraging efficiency. We assessed how the reduction of seed resources provoked by cattle grazing affected different properties of seed-eating bird flocks in woodlands having the same structural characteristics but differing in seed abundance. Under lower availability of grass seeds (i.e. under grazing) flocks were smaller and less rich, and birds showed a lower flocking propensity. This pattern could be explained by three non-exclusive hypotheses. Food reduction caused by grazing (i) decreases the number of seed-eating birds, and concomitantly generates smaller flocks; (ii) reduces the density of nuclear species, decreasing the group cohesion in large flocks; (iii) makes large flocks less attractive by increasing individual competence for food. Our results provide evidence that cattle grazing affect seed-eating birds' interactions, and suggest the importance of understanding flocking behavior to bring about management actions.

Keywords: Winter desert flocks, Seed-eating birds, Grazed woodland, Flock structure, Nuclear species

Introduction

Conservation biology is increasingly concerned with preserving interactions among species and individuals facing anthropogenic change (e.g., Bertiller et al. 2009; Valiente-Banuet et al. 2015; Zou et al. 2018). Bird flocks are an important focus of conservation research because flocks would not be merely a group of individuals flying together but an association of highly interacting individuals which increase foraging efficiency and/or obtain anti-predator benefits (Goodale et al. 2017). Both advantages could finally improve fitness (Jullien and Clobert 2000; Goodale et al. 2017). Flocking would increase foraging efficiency because flock members would be more efficient finding food patches than solitary individuals (Krebs 1973), avoiding previously exploited areas (Beauchamp 2005), and/or feeding on insects that jump because other members of the flock disturb them (Satischandra et al. 2007). Predation risk would be reduced by using information about the presence of predators provided by other individuals (Lima 1995), by the dilution effect (Hamilton 1971), and/or by the physical disturbance of predators by many birds (Templeton et al. 2005). If human perturbation was to reduce food-resource availability or to increase adult bird predation, it is intuitive to expect an increase of bird flocking in degraded environments. However, human activity may have other effects on bird communities (e.g., changes in bird richness and/or abundance) that can alter this prediction. In recent years, some studies have explored anthropic effects on mixed-species bird flocks, mainly focusing on their response to fragmentation (e.g., Stouffer and Bierregaard 1995; Maldonado-Coelho and Marini 2000; Tellería et al. 2001; Sridhar and Sankar 2008; Cordeiro et al. 2015) but also to deforestation (Shirar and Sanker 2008), urbanization (Lee et al. 2005) and livestock grazing (Knowlton and Graham 2011). Despite theoretical expectations,

general patterns showed that flock size, richness and density of flocks decrease when environmental perturbation increases. Studies that analyzed human impact on flocks were carried out in tropical and northern temperate environments, where flocks are comprised mainly of insectivorous birds, and where nuclear species (i.e., species that appear to facilitate flock formation, lead groups, and occur in a high proportion on flocks; Goodale and Beauchamp 2010) are also insectivores (Zou et al. 2018). Current literature about other trophic guilds of birds is scarce, and there are no studies about anthropogenic effects on flocks of seed-eating bird species in desert environments.

In ungrazed open woodlands of the central Monte desert, flocks are formed in autumn and winter by aggregation of seed-eating birds, which represent 96% of all individuals recorded in flocks (Zarco and Cueto 2017). The size (number of individuals) and composition of wintering flocks are variable, including monospecific and mixed-species flocks (Zarco and Cueto 2017). Two seed-eating species (Rufous-collared Sparrow *Zonotrichia capensis* (Statius Müller, 1776) and Ringed Warbling-finch *Microspingus torquatus* (D'Orbigny and Lafresnaye, 1837)) form large monospecific flocks, and behave as nuclear species in mixed-species flocks (Zarco and Cueto 2017).

Medium to large grass seeds are the selected and preferred food for seed-eating birds in the Monte desert (Cueto et al. 2006; Marone et al. 2008; Camín et al. 2015). Cattle grazing reduces the grass stratum, the number of spikes, and the number of grass seeds in the soil bank at local (Gonnet 2001; Pol et al. 2014) and regional scales (Sagario et al. *unpubl. data*), with medium and large seeds the most affected. If flocking is a strategy to increase food finding efficiency in the Monte desert, then changes in food availability could have a great impact being on the flocking behavior of seed-eating birds. For example, in the face of decreased availability of grass seeds in grazed woodland, flocking propensity may increase because finding the preferred seeds may be

difficult. However, grazing has been associated with lower species richness and abundance of seed-eating birds in the Monte desert (Marone 1991; Gonnet 2001; Pol et al. 2014; Sagario et al. *unpubl. data*) and this may negatively influence flocking propensity, as well as the size and species composition of the flocks. In this paper, we inquire about the effect of grazing on different variables describing the flocking behavior of seed-eating birds in the central Monte desert, and we propose plausible explanatory hypotheses to the observed patterns.

Methods

We conducted our study in the Ñacuñán reserve (34° 03' S, 67° 54' W, a UNESCO Man and the Biosphere Reserve) and in the cattle ranch “El Doménico” (which adjoins the reserve) in the central Monte desert, Mendoza Province, Argentina. The reserve has been effectively excluded from cattle grazing since 1972, when it was fenced. The climate is dry and temperate, with hot summers and cold winters. On average, > 75% of annual rainfall (349 mm, n = 31 years) occurs during the grass-growing season (October–March), although precipitation varies widely between years. The main habitat type in Ñacuñán Reserve and “El Doménico” cattle ranch is the open woodland or “Algarrobal”, dominated by algarrobo dulce (*Prosopis flexuosa* DC.) and chañar (*Geoffroea decorticans* (Gillies ex Hook. & Arn) Burkart.) trees. The shrub stratum is composed mainly of jarilla (*Larrea divaricata* Cav.), and the herbaceous stratum by perennial grasses and forbs.

We selected two sites (ungrazed and grazed, inside and outside the reserve, respectively) with similar arboreal and shrubby structure (Zarco 2016). In the study area and over the study period (July 2013 and 2014, austral winter), abundance of medium to

large grass seeds in the soil seed bank in the grazed site was 94% (2013) and 53% (2014) lower than in the ungrazed site (Sagario et al. *unpubl. data*). Also, the abundance of grass spikes was 94% lower in grazed than in ungrazed sites (Pol et al. 2014).

We sampled bird populations and estimated bird density using the strip transect method (Ralph et al. 1993). Transects were set up at a minimum distance of 1 km from the fence that demarcates the reserve (i.e., separates grazed and ungrazed woodlands). Each transect was 500 m long, and the strip band was 50 m on each side of the line. Transects were set up at a minimum distance of 150 m from each other. In grazed and ungrazed sites the same number of transects were surveyed (17 in each site in 2013 and 14 in each site in 2014). Transects were surveyed during the 4 hours after dawn by the same observer (AZ), for 35 to 45 minutes (excluding time spent watching flocks, see below).

We defined a flock as at least three individuals moving together in the same direction and exceeding distances of 15 m, with flock members < 10 m apart, and without an indication that the birds were attracted by a concentration of food (Ippi and Trejo 2003; Zarco and Cueto 2017). We followed flocks for a maximum of 10 minutes, and then we continued walking the transect. For this study, we only considered seed-eating passerines (insectivores represent 2% of flock members in central Monte desert, Zarco and Cueto 2017). Family groups of Many-colored Chaco Finch *Saltatricula multicolor* Burmeister, 1860, defined by small groups that included juveniles and adults which exhibited defense behavior in front of the observer (Zarco and Cueto 2017) were not included in the analysis as flocks.

We estimate flock size (number of seed-eating individuals in the flock), and flock richness (number of seed-eating species in the flock) and, to evaluate differences in these variables between grazed and ungrazed woodlands, we employed generalized

linear mixed models (GLMMs), with year as a random factor. We assumed a negative binomial distribution of errors for size, and a Poisson distribution for richness, and used a logit link function in those models. We used the lme4 (Bates et al. 2015) and glmmADMB (Skaug et al. 2012) packages in R (R Development Core Team 2016) for statistical analyses.

We also estimate flock density as the number of flocks divided by the sampled area, and total, mixed, and monospecific flocking propensity as the total number of individuals of a species that participated in both, only in mixed, and only in monospecific flocks, divided by the total number of individuals (solitary + pairs + birds in monospecific or mixed flocks) of that species. To evaluate differences in flocking propensity between grazed and ungrazed woodlands for the three most abundant seed-eating species (Rufous-collared Sparrow, Ringed Warbling-finch and Many-colored Chaco Finch), we performed a Test for Differences for Two Proportions (Zar 2010), using InfoStat (Di Rienzo et al. 2012). Also, in each site we calculated flock number per 100 individuals. We finally computed mixed flocking proportion as the number of individuals of one species in mixed flocks divided by the number of individuals of such species in monospecific plus mixed flocks.

Results

We found 2977 seed-eating birds, 90.3% of them in ungrazed woodlands. The size (GLMM: $F = 2.268$, $P = 0.023$, Fig. 1) and richness (GLMM: $F = 2.405$, $P = 0.016$, Fig 2) of seed-eating bird flocks were lower in grazed than in ungrazed woodlands. Three species of seed-eating flock members were found in grazed woodlands (Rufous-collared Sparrow, Many-colored Chaco Finch and Ringed Warbling-finch), and seven

in ungrazed woodlands (Rufous-collared Sparrow, Many-colored Chaco Finch, Ringed Warbling-finch, Cinnamon Warbling-finch *Poospiza ornata* (Leybold 1865), Common Diuca-finch *Diuca diuca* (Molina 1782), Carbon Sierra-finch *Corydospiza carbonaria* (Lafresnaye and D'Orbigny 1837) and Mourning Sierra-finch *Rhopospina fruticeti* (Kittlitz 1833)) (Table 1).

We found lower flock density in grazed (0.041 flocks/ha in 2013 and 0.086 flocks/ha in 2014, 19 flocks in both years) than in ungrazed woodlands (0.159 flocks/ha in 2013 and 0.286 flocks/ha in 2014, 67 flocks in both years). However, we found a greater number of flocks relative to the number of individuals in grazed (6.6 flocks per 100 individuals) than ungrazed (2.5 flocks per 100 individuals) woodlands.

Mixed flocking proportion was smaller in grazed than ungrazed woodlands (Table 1). The proportion of seed-eating birds engaged in any type of flock was smaller in grazed than in ungrazed woodlands ($Z = 0.297$, $P < 0.001$, Fig. 3a). Total and mixed flocking propensity was substantially smaller in grazed than ungrazed woodlands for Rufous-collared Sparrow ($Z = 0.319$, $P < 0.001$ and $Z = 0.321$, $P < 0.001$, respectively), but monospecific flocking propensity for this species was similar in both sites ($Z = 0.002$, $P > 0.99$, Fig. 3b). Total ($Z = 0.313$, $P < 0.001$), mixed ($Z = 0.388$, $P < 0.001$) and monospecific ($Z = 0.076$, $P = 0.009$, Fig. 3c) flocking propensity of Ringed Warbling-finch were smaller in grazed than in ungrazed woodlands. Many-colored Chaco Finch did not form monospecific flocks, and participated in mixed-species flocks in the same proportion in both sites ($Z = 0.091$, $P = 0.411$, Fig. 3d).

Discussion

Grazing decreases flock size and richness, flock density, flocking propensity, and mixed flocking proportion, but increases the number of flocks per 100 individuals. In the face of a decrease in availability of grass seeds in grazed woodland we expected an increase in flocking propensity but found the opposite pattern, which suggest that food reduction had effects on bird flocks different from increasing collaborative behavior.

The pattern described could be explained by territorial surface reduction under habitat perturbation (e.g., Thiollay 1992; Van Houtan et al. 2006), but Monte desert winter flocks are non-territorial (Sagario and Cueto 2014; Zarco 2016), and therefore the changes observed in flocks could not be attributed to a reduction in the defended surface or territory. The pattern can also be explained by changes in predation risk in grazed areas, since anthropic disturbance could increase the exposure of flocks to predators and, consequently, change the conformation of the flocks (e.g., Latta and Wunderle 1996; Thiollay 1999; Borah et al. 2018). We, notwithstanding, dismiss a predator effect on flocking for two reasons. On the one hand, predation risk perceived by birds depends largely on plant structure (Lima and Dill 1990; Whittingham and Evans 2004), and both grazed and ungrazed woodlands in our study area have similar woody structure (Zarco 2016; Pol et al. 2014). On the other hand, in the central Monte desert adult bird predation is principally aerial in winter, because reptiles are not active, micro-mammals do not prey on adult birds (Giannoni et al. 2005; Lanzone et al. 2012), and native carnivores rarely prey on adult birds (González del Solar et al. 1997; Bisceglia et al. 2008). In Ñacuñán we detected the presence of birds of prey: American Kestrel *Falco sparverius* Linnaeus 1798, Spot-winged Falconet *Spizapteryx circumcincta* (Kaup 1852), Austral Pygmy-owl *Glaucidium nana* (King 1828) and Grey-bellied Shrike-tyrant *Agriornis micropterus* (Gould 1839). However, they had very low and similar abundance in both grazed and ungrazed woodlands (Zarco 2016).

Food reduction –in a context where it does not increase flocking propensity– would be the more plausible reason to explain the general decrease of abundance of seed-eating birds as well as the decrease in flocking in grazed woodlands. There are three (non-mutually exclusive) hypotheses that could explain the observed pattern based on food reduction. Firstly, the reduction in total numbers of seed-eating birds in grazed woodlands can generate smaller flocks, with less richness. Reduction in winter abundance of seed-eating birds in grazed woodlands of the central Monte desert had been observed previously at local (Marone 1991; Gonnet 2001) and regional (Sagarío et al. *unpubl. data*) scales. Previous observations suggest that Monte desert flocks are highly mobile (Sagarío et al. 2014; Zarco 2016), but flocks are dynamic because they are formed by the constant addition of solitary members or small groups (Zarco and Cueto 2017). A positive relationship between flock size and population density has been also reported in other systems (e.g., Krause and Ruxton 2002; Beauchamp 2011). Lower abundance of seed-eating birds may generate a reduced rate of encounters between individuals in grazed woodlands, and this could explain the differences in density and structure of the flocks in both sites.

Secondly, as observed in previous studies involving mixed-bird flocks (e.g., Stouffer and Bierregaard 1995; Maldonado-Coelho and Marini 2000; Tellería et al. 2001; Zuluaga and Rodewalt 2015), a reduction in the density of nuclear species can affect the structural components of flocks (size, composition, cohesion). The lower abundance of individuals of Rufous-collared Sparrow and Ringed Warbling-finch (regular and nuclear species, Zarco and Cueto 2017) in grazed woodlands could explain differences between flocks on grazed and ungrazed woodlands. It has been observed in cattle-free woodlands of Monte desert that mixed-species flocks without Ringed Warbling-finch are smaller than those including this species (Zarco and Cueto 2017). A

decrease in nuclear species could particularly affect species which move exclusively in mixed-species flocks (for example, 97% of winter individuals of Cinnamon Warbling-finch form flocks following the nuclear Ringed Warbling-finch, Zarco and Cueto 2017). Reduction in monospecific flock proportion of Ringed Warbling finch in grazed woodland could increase this effect, because mixed-species flocks form from individuals of other species joining monospecific groups of Rufous-collared Sparrow and Ringed Warbling Finch (Zarco and Cueto 2017). This explanation is strongly linked to the previous one, because the most abundant species (Rufous-collared Sparrow and Ringed Warbling-finch) are also the flock nucleus in our system.

Lastly, grazing could affect competition for food. If food decreases considerably in a habitat, forming larger groups may not be an effective strategy because larger groups would increase competition (Hutto 1988; Fernandez-Juricic *et al.* 2004). Moving in smaller groups or even in a solitary way may have the advantage of decreasing both intra- and interspecific food competition when birds find a food patch (Giraldeau and Beauchamp 1999). This hypothesis would explain not only a smaller size of flocks, but also the greater number of flocks –relative to the number of individuals– in grazed woodlands.

Previous studies suggest that flocking affects individual fitness (Julien and Clobert 2000), and that the breakup of flocks can have long term effects on bird populations (Mammides *et al.* 2015). In the central Monte desert, flock structure is influenced by food availability, which is decreasing as a result of grazing. Our findings, of higher incidence of gregarious behavior of the most abundant species in ungrazed woodlands, provide valuable information about the indirect consequences of land management practices. In the central Monte desert, woodlands occupy more than two million hectares, and only 0.6% of this surface is protected against cattle grazing

(Villagra et al. 2010). Grazing could have a large-scale effect on some bird species that group in flocks in autumn and winter. Environmental policies to mitigate grazing effect on wildlife would benefit if mechanisms involved in the impoverishment of flocks are unveiled. The role of some demographic variables (e.g., flocking effect on adult survival), and responses to another anthropic disturbances such as fire could help unveil those mechanisms and highlight the importance of flocking behavior for bird populations.

Acknowledgments

We would like to thank to CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas), Universidad de Buenos Aires, the Ñacuñán forest ranger team, and the administrator of “El Doménico” cattle ranch Lucas Merljak. We thank R.M. Brigham, H. Guderley, and one anonymous reviewer for helpful comments that greatly improved our article. Holly Pickett helped us with the English language editing of the manuscript. This research was conducted under authorization of the Dirección de Recursos Naturales Renovables of Mendoza, Argentina (resolution 2012-1243). Funding was provided by Neotropical Grassland Conservancy (Student Grant Program 2014) and ANPCYT (Agencia Nacional de Promoción Científica y Tecnológica, PICT 2176). Contribution number 105 of Desert Community Ecology Research team (ECODES).

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Table 1 Winter density (individuals / ha) and mixed flocking proportion of wintering seed-eating birds in grazed and ungrazed woodlands of central Monte desert, Argentina.

Numbers are averages of strip transect records in 2013 and 2014. The symbol “—” denotes zero individuals observed.

Species	Woodland	Non-flocking birds	Monospecific flocks	Mixed-species flocks	Mixed flocking proportion
Rufous-collared Sparrow, <i>Zonotrichia capensis</i>	Ungrazed	0.331	0.581	5.212	0.90
	Grazed	0.265	0.069	0.377	0.84
Ringed Warbling-finch, <i>Microspingus torquatus</i>	Ungrazed	0.204	0.092	2.200	0.96
	Grazed	0.108	0.031	0.135	0.81
Many-colored Chaco Finch, <i>Saltatricula multicolor</i>	Ungrazed	0.473	—	0.258	1.00
	Grazed	0.085	—	0.031	1.00
Cinnamon Warbling-finch, <i>Poospiza ornata</i>	Ungrazed	0.012	—	0.408	1.00
	Grazed	—	—	—	—
Carbon Sierra-finch, <i>Corydospiza carbonaria</i>	Ungrazed	0.246	0.092	0.177	0.66
	Grazed	—	—	—	—
Mourning Sierra-finch, <i>Rhopospina fruticeti</i>	Ungrazed	—	—	0.004	1.00
	Grazed	—	—	—	—
Common Diuca-finch, <i>Diuca diuca</i>	Ungrazed	0.004	—	0.050	1.00
	Grazed	0.008	—	—	—

Fig. 1. Flock size (number of seed-eating individuals in a flock + SE) in ungrazed ($n = 67$) and grazed ($n = 19$) woodlands in central Monte desert, Argentina. Asterisk indicate significant difference for GLMM ($P < 0.05$).

Fig. 2. Flock richness (species number of seed-eating birds in a flock + SE) in ungrazed and grazed woodlands in central Monte desert, Argentina. Asterisk indicate significant difference for GLMM ($P < 0.05$).

Fig. 3. Proportion of flocking and non-flocking wintering seed-eating birds in the central Monte desert, Argentina. Proportions of a) all seed-eating birds, b) Rufous-collared Sparrow, *Zonotrichia capensis*, c) Ringed Warbling-finch, *Microspingus torquatus*, and d) Many-colored Chaco Finch, *Saltatricula multicolor* are shown. Black bars indicate proportion of birds in mixed and monospecific flocks (a) or in mixed-species flocks (b, c, and d), grey bars indicate proportion of birds in monospecific flocks, and white bars indicates proportion of non-flocking birds. Numbers above the bars indicate the total number of observed birds.

Figure 1

Figure 2

Figure 3