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Euphonia plumbea (macho)
Foto: Daniel Lane.

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Habitat use and seasonality of birds in the Peruvian puna with an emphasis on peatlands (bofedales)

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ABSTRACT

Habitat associations and seasonality patterns are poorly known for many of Peru's birds. This basic ecological information is used for many scientific inquiries and also by regional land managers tasked with maintaining habitat for many species. The puna grasslands of Peru are relatively species poor when compared to the lowland rainforests, but there is a high degree of endemism, which adds weight to management and conservation decisions. We performed line transects in the Peruvian puna for both the wet and dry seasons to determine habitat associations and seasonality with an emphasis on peatlands (bofedales). We analyzed 38 species and 6492 habitat assignments for patterns of habitat associations. This analysis revealed both generalists and specialists for puna habitat types and strong seasonality for several species

Key words: habitat associations, seasonality, Peru, puna, birds, bofedales, peatlands.

RESUMEN

Las asociaciones de hábitat y patrones de estacionalidad son poco conocidos para muchas especies de aves del Perú. Esta información ecológica básica se utiliza para muchas investigaciones científicas y es usada también por los encargados de gestionar las tierras regionales y por los encargados de mantener el hábitat de muchas especies. Los pajonales de puna del Perú son relativamente pobres en especies, comparados con las selvas tropicales de tierras bajas, sin embargo tienen un alto grado de endemismo, lo cual agrega peso a las decisiones de manejo y conservación. En este trabajo realizamos transectos lineales en la puna peruana, tanto en la estación húmeda como seca, para determinar las asociaciones de hábitat y la estacionalidad, con énfasis en las turberas (bofedales). Analizamos 38 especies y 6492 asignaciones de hábitat para determinar los patrones de asociación de hábitats. Este análisis reveló la presencia, tanto de especies generalistas como especialistas para los tipos de hábitat de puna, así como la presencias de una

fuerte estacionalidad para varias especies.

Palabras claves: asociación de hábitats, estacionalidad, Peru, puna, aves, bofedales

INTRODUCTION

The relationship between habitat and birds has long held the attention of researchers working to understand ecological principles and processes (Grinnell 1917, Lack 1937, MacArthur 1958, Wiens 1989). Birds are excellent organisms for the study of habitat selection because they are highly mobile and thus encounter many habitats from which to choose (Cody 1985). Presence in a habitat is de facto evidence for habitat selection or some component therein. Habitat-related decisions influence their foraging success (Davis 1982) and productivity (Martin 1998), which ultimately may shape their evolution. From a more applied perspective, these life history details are used to develop distribution and population estimates, which are used by conservation biologists, population geneticists, land managers, and policy makers.

The Neotropical avifauna is species rich (~3500 species) and riddled with knowledge gaps, a result of relatively few researchers and remoteness. Grassland birds in the Neotropics are no exception, with basic ecological information lacking for many species, e.g. geographic range limits, habitat associations, and phenology. Vuilleumier (1986) identified 166 bird species as the combined paramo/puna core breeding group, with another 35 migratory species recorded in the region either from North America (30 species) or South America (5 species). Of the core breeding group, 48 of 166 (29%) species were identified as endemic, and another 21 species (13%) were "nearly endemic". Of the six Neotropical grassland types recognized by Stotz *et al.* (1996), the puna is considered to be one of two centers of diversity for grassland birds with a relatively high degree of species-level endemism (Müller 1972, Cracraft 1985, Parker *et al*. 1982, Vuilleumier 1986, Fjeldså and Krabbe 1990). Because its high degree of endemism and the anthropogenic activities in the region (e.g. resource extraction, intensive pastoralism, climate change, water projects), both the Central Andean and Central Andean Wet Puna were identified as key terrestrial ecoregions in a recent analysis of strategies for maximizing biodiversity conservation (Loyola *et al*. 2009). Similarly, the World Wildlife Fund (2006) designated these two ecoregions as "vulnerable".

Located high in the Andes, puna grasslands occur above the alpine tree line (~4000 m) in terrain described as alpine tundra (Lomolino *et al*. 2005). The puna covers approximately 586,100 km^2 from central Peru through Bolivia to northwestern Argentina and northern Chile. The puna spans the north-south and east-west precipitation gradients and is subdivided into three ecoregions characterized by their climate: the Central Andean dry puna occurring in the south and west, the Central Andean puna occupying the middle range of the precipitation gradient in Peru and Bolivia, and the Central Andean wet puna occurring in the northern and eastern extremities of the puna. Combined, the puna is set apart from the equatorial paramo ecoregion by distinct wet and dry seasons (Weberbauer 1936, Pulgar Vidal 1941).

Within the puna ecoregion, several distinct habitats occur (Fig. 1). The most extensively studied is the *Polylepis* woodland, so named for the tree genus that occurs as island-like patches of short trees on steep slopes or inaccessible areas well above the elevation where most trees can exist, in defiance of the treeline concept (Fjeldså 1987, Fjeldså

1992, Herzog *et al*. 2003, Lloyd and Marsden 2008). This habitat is currently a small fraction of the puna and remains under intense pressure from human activity as a source of wood for cooking and construction. *Polylepis* woodland conservation efforts have made significant strides, and areas targeted for conservation were recently identified (Fjeldså and Kessler 1996, Fjeldså 2002, Benham *et al.* 2011). In contrast to the *Polylepis* woodlands, the remaining puna habitats and faunal associates are poorly studied. We have excluded the *Polylepis* habitat from this study as it is treated well elsewhere.

Figure 1. Habitat types in the puna to which individual bird observations were assigned: (a.) bunchgrass e.g. *Stipa* and *Festuca;* (b.) short grass e.g. *Calamagrostis* and *Dicanthelium*; (c.) peatland (bofedal) e.g. *Distichia*, *Oxychloe*, and *Plantago*; (d.) laguna; (e.) stream; (f.) rocky; and (g.) bare ground.

The other woody-stemmed habitat is the shrub-dominated *tola* that occurs on well-drained slopes. Otherwise, bunchgrass and short-grass habitats characterize the puna. Found throughout the vast puna grassland is an archipelago of wetland habitats that includes cushion plant peatlands (locally called *bofedales*), reed beds, open water *lagunas* such as lakes and ponds, and small to medium streams (Stotz *et al.* 1996). Finally, bare ground habitat occurs in large and small patches. The smaller often circular recessed patches are a result of temporary vernal pools drying up and large expanses of bare soil occurs at the higher reaches of the puna where even the hardiest of grasses have yet to take hold. Of these habitats, the permanent cushion-plant peatlands are particularly interesting because they are permanent wetlands in a highly seasonal ecoregion and have received little attention. Both Squeo *et al.* (2006) and Telleria *et al.* (2009) argued for the importance of bofedales and noted the dependence of local human communities that have practiced pastoralism for hundreds of years on these permanent wetlands. Perhaps most important is the water that is filtered, stored, and meted out by these wetlands for humans, their animal stock, and wildlife, especially in the dry season.

The high Andes have attracted many pioneering ornithologists: Chapman, Morrison, Koepcke, Dorst, Pearson, and O'Neill to name a few. They discovered new species, postulated the origins of the Andean avifauna, and established an impressive foundation upon which subsequent researchers have relied heavily. Anecdotal evidence of habitat associations developed from years of fieldwork and data compiled from natural history collections was presented by these and many others. This is the only information available for two species of conservation concern found in these peatlands. The White-bellied Cinclodes (*Cinclodes palliatus*) and the Diademed Sandpiper-Plover (*Phegornis mitchellii*) are both considered resident and specialists of high Andean peatlands. Still, a quantitative approach to understanding puna habitat associations is lacking. Specifically, we wanted to know which species were using which habitats and when? Do these habitat associations change with the wet and dry seasons?

METHODS

Study sites

Bird occurrence was sampled at 38 study sites in the puna of central and southern Peru (Fig. 2). Study sites were selected using a non-random convenience sample (Cochran 1977) due to logistic constraints such as few roads in the highlands and time needed to access remote locations. Sites with bofedales were selected in central and southern Peru between 4000-5000 m elevation (Fig. 3) by using satellite imagery and topographic maps from the Instituto Geográfico Nacional. All sites had moderate to strong grazing pressure from sheep, alpaca, and llamas. Because pastoralism has likely dominated the landscape for millennia (D'Altroy 2000), trying to find ungrazed sites is extremely difficult and beyond the scope of this study. In the second year of surveys we characterized the study sites using Nott *et al.'s* (2003) Habitat Structure and Assessment protocol. Finally, we took water pH measurements at each study sites as part of the site characterization.

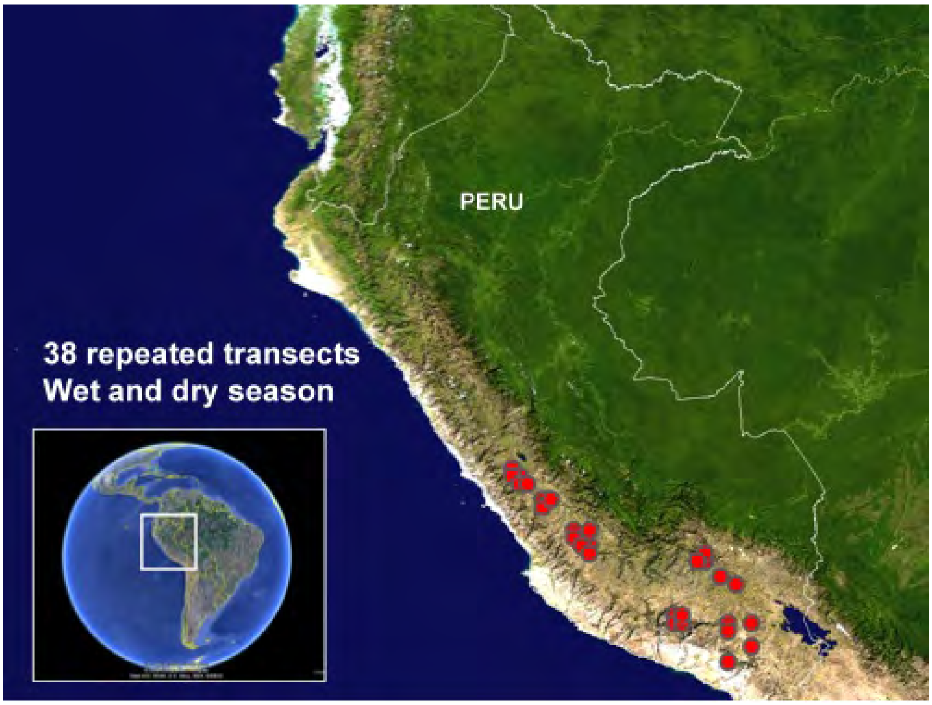

Figure2. The study was completed in Peru, specifically the Central Andes. Study sites are indicated with red circles.

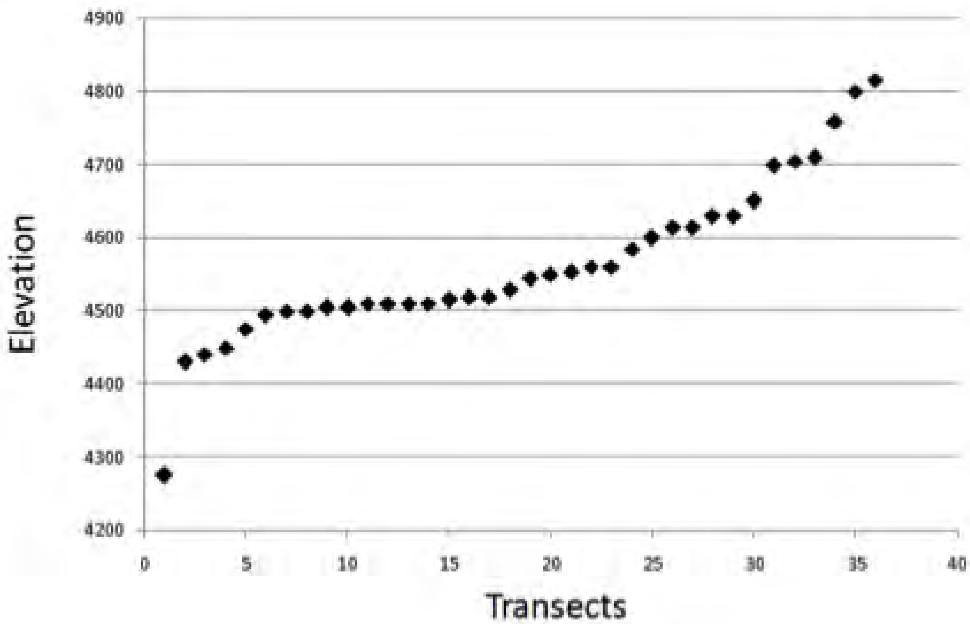

Figure 3. Elevation (meters) of transect sites (N=38).

Transect surveys

To quantify bird-habitat relationships, transect surveys that averaged 1.1 km (range 0.5 to 1.75km) were conducted in both wet (November-April) and dry seasons (May-October) in 2008 and 2009 between the hours of 0900 and 1600. Nearly all birds detected by sight or sound were identified to species, but a few were identified to genus only. Detections were limited to within 100 m of the transect line. The majority of transects were completed by Richard E. Gibbons (REG), but Phred M. Benham (PMB) completed several in 2008. Both PMB and REG spent several weeks together in the Peruvian highlands during 2007 to become familiar with the avifauna and to scout study sites. REG used a 10X Zeiss Victory binocular and PMB used a 8X Zeiss Victory binocular. We reported all visual and auditory detections and assigned each detection to one of seven habitat types: peatland (bofedal), short grass (cesped), bunch grass, rocky ground, bare ground, standing water, and stream.

Statistical analyses

All analyses were completed with the SAS statistics package. Rare species were dropped from the analysis to minimize bias. To do this objectively, we used an arbitrary threshold of 1% of total counts and 2% of the sum to bring the data closer to a normal distribution. Data were normalized by log transformation and by adding one to each cell in the database to account for the log of zero issue. Exploratory factor analysis (Johnson 1998), a type of principal component analysis, was used to identify patterns within the transect data. The data included counts of species within the seven habitat types during the two wet and dry sampling periods. The factors were rotated orthogonally using the varimax rotation method. This technique permitted easier interpretation of the factors while maintaining the accounted variance proportion for the entire data set. After the number of factors for the model was selected, mixed models were performed for each orthogonal factor separately to determine relationships between the factors and habitat and season. Habitats and seasons were fixed effects, whereas year and transect were random effects. We set the significance level at 0.05 ($\alpha = 0.05$), and pair-wise contrasts were tested with Tukey adjustments.

RESULTS

Study Sites

The evaluated habitats were in the Tropical Alpine Wet Tundra and Subtropical Alpine Wet Tundra, which generally have rugged topographic relief ranging from hilly to undulating, the latter mainly glacially formed. The soils were acidic, constituting Paramosols, Paramoandosols, Lithosols, Gleysols and in places of poor drainage, Histosols (organic) (ONERN 1976). The proportion of habitats surveyed was skewed toward the short grass and bofedal habitats (Fig. 4) with the remaining habitat types comprising small percentages. A notable difference documented between the southern (Puno, Moquegua, Arequipa, Cusco) and central (Huancavelica and Junín) study sites was the landscape context. Southern study sites tended to be in narrow valleys whereas northern study sites tended to be in wider valleys and hilly terrain.

Grasses were consistent across sites with *Gentianella*, *Sedifolia*, *Gentiana*, *Werneria pygmaea*, *Hypsela reniformis*, and *Ourisia* present. A species composition dichotomy occurred between the central Peru and southern Peru sites. In Central Peru the listing of species varied with the appearance of *Plantago rigida*, *Oreithales integrifolia*, and *Werneria pectinata*, which has distribu

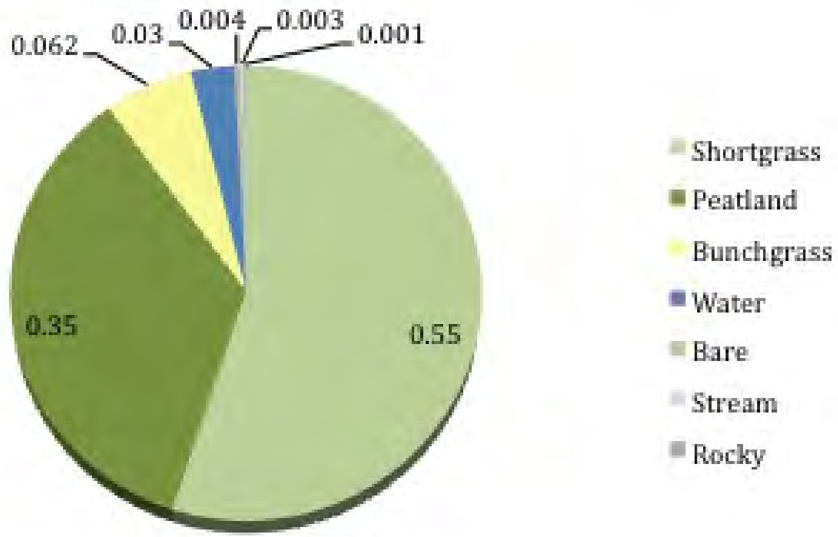

Figure 4. Habitat types are shown with percentage of study site area. Vegetation characterizations were completed in the dry season so water is underrepresented

tion that extends into the highlands of northern Peru.

Among the bofedal habitats sampled, the most conspicuous and diagnostic feature was the presence of a top layer of organic matter (peat). The primary peat producers are two rush species that have a cushion-like form: *Distichia muscoides* (whole latitudinal gradient) and *Oxychloe andino* (only in the south). Of the 38 transects evaluated, 33 included some type of peatland within the assessment area. Eight peatland types were identified (Fig. 5) after site characterization were analyzed using the criterion that the dominants were peat producing species. The peatland types were not accounted for in this study, but are reported here for the benefit of future studies. Analyses of habitat types were constrained by habitat structure rather than replacement species composition. The regional variation among peatlands is noteworthy and warrants further investigation.

As shown in Figure 5, *Distichia muscoides* peatlands (Tur_Dis_mus) are distributed throughout the latitudinal range and precipitation gradient, spanning the wetland systems to the greatest extent (86.2%). Compared to other types of peatlands and vegetation, this peatland type was matched only by the *mixed* peatland and *Oxychloe andina* and *Distichia muscoides* (Tur_Dis_Oxy) types with an area totaling 87% of southern transects. The presence of mixed-species peatlands and the emergence of pure *Oxychloe andina* peatland in the south may be the result of ecological replacement. The pH values (Fig. 5) varied slightly from neutral at the central Peru sites (fens) to slightly acidic in the south (bogs) coinciding with peatland type turnover.

Bird detections

We assigned habitat associations to 7345 individuals of 98 species detected during line transects in both wet and dry seasons (Table 1). The data-cleaning step reduced the number of species to 38 while keeping the majority of observations (6492) (Appendix 1.). To review, we used factor analysis to identify patterns in the bird observation data, and mixed models were used to determine the pattern drivers.

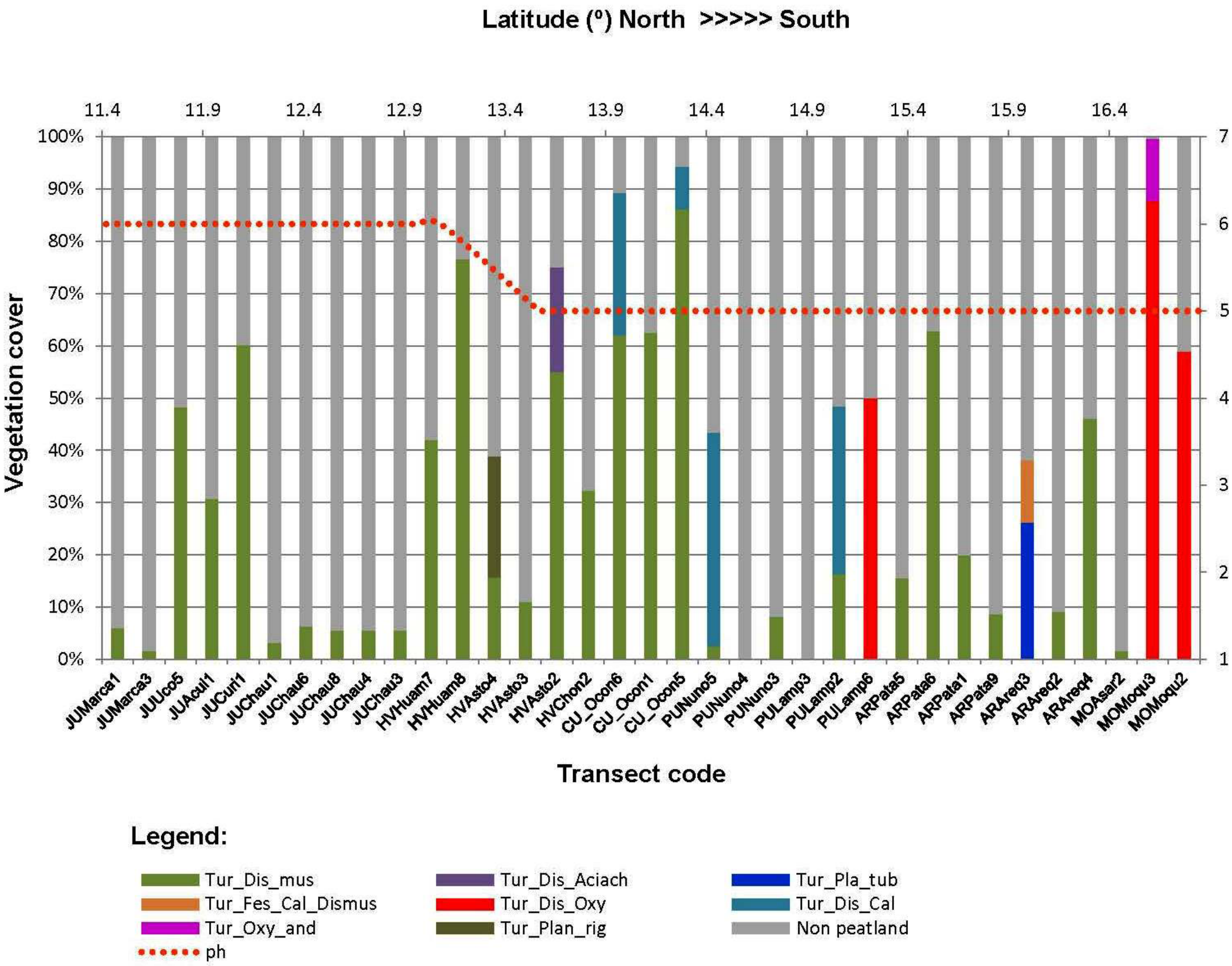

Figure 5. Occurrence of different peatland types by latitude with pH included as a dotted red line.

Eigenvalues in the factor analysis represent the variances in the original dataset captured by the corresponding factors (Appendix 2). The factors were sorted by their eigenvalues, with the first factor accounting for the most variation, the second factor accounting for the second most, and so on. A scree plot (Appendix 3) was constructed by plotting each eigenvalue against its corresponding factor. After viewing the results, we chose a 6-factor model because this captured the vast majority of the variance with the fewest number of factors. This leveling off of variance can be seen in the scree plot as the "elbow" between 6 and 8 variables.

Post-orthogonal rotation factor loadings are summarized as species groups (Table 2). A 0.5 threshold was applied, i.e. if a species' loading on the factor was greater than 0.5, it was considered to be in that group. To determine the drivers of the factor groupings, mixed models were constructed with habitat and season treated as fixed effects and year and transects treated as a random effects. Mixed model analysis results are listed as Appendices 4 and 5. The Tukey grouping letters in Appendix 4 indicate whether a particular habitat type contributed to significant differences in the response variable. The effect of season for each factor grouping is shown in Appendix 5 with Factors 2, 3, and 4 having significant seasonality.

Finally, Appendix 6 illustrates that the habitat-season interaction effect was significant in factors 2-5. The vertical bars for the bare ground and bunch grass are wider than others because this habitat was present in only one year, i.e. it was added for the second year of data collection after evaluation of surveyed habitats in the first year.

DISCUSSION

Factor Analysis

Species in the Factor 1 grouping were associated with the laguna habitat (lakes and ponds) and lacked a strong seasonal effect. The association of open water and a grebe (*Podiceps occipitalis*), three ducks (*Oxyura jamaicensis*, *Anas puna*, and *Anas flavirostris*), a rail (*Fulica gigantea*), a gull (*Chroicocephalus serranus*), and a flamingo (*Phoenicopterus chilensis*) is of course unsurprising but provided some confidence in the analysis. The mixed models did not find a significant seasonal effect for this factor despite a pronounced seasonal disparity in abundance for two of the species, *Phoenicopterus chilensis* and *Phalaropus tricolor* (Fig. 3). *Phoenicopterus chilensis* has both resident and migratory populations, and the raw values we detected could reflect an influx of wintering birds from the south. *Phalaropus tricolor*, a Nearctic-Neotropical migratory shorebird, grouped with factor 1 just above the 0.50 threshold with a value of .57, but had higher loadings with factor 3, the seasonal peatland grouping, which is addressed below.

The ten species with high Factor 2 loadings were associated with the peatland habitat, and detections were seasonally skewed toward the dry season according to the mixed model analysis. This could be the result of a post-breeding population increase following the wet season, when most breeding occurs. It also could be the result of birds concentrating in these permanent wetlands in the dry season when surrounding grasslands and ephemeral water sources have dried up. If the latter is true, then this "oasis effect" would increase the need for the study and conservation of these isolated wetlands. Squeo *et al*. (2006) called for further study of these poorly understood and important habitats.

The five species with high Factor 3 loadings were associated with both bofedales and laguna habitats, and their detections were skewed toward the wet season. Three of these species are Nearctic-Neotropic migratory shorebirds overwintering in the peatlands and exhibiting a near-complete withdrawal from the Neotropics in the dry season. The other two species are Neotropical ducks restricted to the temperate high Andes and southern South America. Whereas the two shorebird species are overwintering in the laguna and adjacent bofedales, the two duck species nest in the warmer wet season. The straddling of the two habitats by these species is sensible given they are either foraging in the laguna habitat as expected for ducks and shorebirds or resting in the adjacent habitat, most often bofedal.

The Factor 4 grouping had five species with high loadings: *Anthus furcatus*, *Geositta tenuirostris*, *Geositta saxicolina*, *Geositta cunicularia*, and *Phalcoboenus megalopterus*. The mixed models indicated these were species associated with the short grass habitat and were seasonally skewed with abundance higher in the dry season. The species with the highest loading in this grouping was *Anthus furcatus*, a "pipit" in the Motacillidae. Most members of the genus (c. 40) are strongly associated with grassland habitats (Tyler 2004). Likewise, *Geositta* species (Furnariidae) are strongly associated with open habitats and grasslands (Remsen 2003). Three species of *Geositta* (*cunicularia*, *tenuirostris*, and *saxicolina*) occurred syntopically during transects in the dry season, presumably the non-breeding season for the *Geositta* occurring in the puna (Remsen 2003). Counts of *G. cunicularia* in short grass increased dramatically in the dry season, nearly doubling from 41 to76 individuals. The pattern for *G. cunicularia* in bofedal habitat was reversed in the wet season, when numbers more than doubled, thus suggesting seasonal movements.

A notable finding in this group was the lack of a single record of *G. tenuirostris* during the wet season. It is considered a resident species (Schulenberg *et al*. 2007, Fjeldså and Krabbe 1990, Remsen 2003), but the data suggested some type of seasonal movement from the upper puna, elevationally or otherwise. A review of *G. tenuirostris* observations submitted to eBird (eBird 2011) during the same period we sampled (February-May) provided several records (N=10) to the contrary with observations as high as 4500 m. This finding prompted a review of completed transects not included in statistical analyses due to incomplete seasonal sampling. The review provided six *G. tenuirostris* detections in dpto. Junin, which contradicts the complete evacuation finding. Nevertheless, counts of *G. tenuirostris* were decidedly higher in the dry season suggesting some movement is possible.

The four species with high loadings on Factor 5, *Diuca speculifera*, *Muscisaxicola albifrons*, *Asthenes humilis*, and *Phrygilus unicolor*, were associated with bofedal, and the mixed model analysis showed no seasonal effects. This result is somewhat contrary to inspection of the raw data and potentially may be the result of information lost in the factor derivation step. Looking at the raw count data for these species provides a different picture. *Diuca speculifera* nearly tripled in the dry season in the bofedal habitat and also tripled in the short grass habitat in the dry season. It seems unlikely that local fledglings would triple the population. So, where were the additional birds in the wet season? Temperatures are warmer in the wet season and upslope migration could account for the discrepancy. For a species known to nest in glacier caves (Hardy and Hardy 2008), this may be worth investigating. The majority of *Muscisaxicola albifrons* observations were in bofedal habitat, and counts increased modestly in the dry season, perhaps a post-reproductive season effect. This signal was considerably more pronounced in the short grass habitat. We recorded ten *M. albifrons* in short grass habitat, eight of which were in the dry season. This reflects a pattern seen in several species in the short grass habitat with seasonally skewed counts in the dry season.

The three species associated with Factor 6, *Phrygilus plebejus*, *Asthenes modesta*, and *Thinocorus orbignyianus*, had positive correlations with grass, bofedal, bunch grass, and bare habitats, and did not show a significant seasonal effect in the mixed model analysis. This could be interpreted as species being generalists in grassy habitats. Similar to Factor 5, the raw scores could suggest a different interpretation. The raw numbers for *Phrygilus plebejus* increase dramatically in the dry season in grassy habitats. This result –as with Factor 5- could reflect the seasonal increase of seeds and prey in the more seasonal short grass habitat. Certainly the possibility of individuals concentrating as a result of seasonal movement is possible, but to corroborate this would require additional fieldwork with marked individuals. This seasonal pattern is even more dramatic in *Thinocorus orbignyianus*, for which counts in short grass and bofedal spiked in the dry season. *Asthenes modesta* was found most commonly in bunch grass habitat, but secondarily was observed at the edge of bunch grass in short grass or bofedal habitats.

Habitat

The study provided information for habitat use in the wet and dry seasons (Table 1 and Fig. 6). In bofedal and laguna habitats, boreal and austral migratory species arrived and departed during their respective non-breeding periods seemingly in an ebb and flow cycle. At the same time, Andean species such as *Lophonetta specularioides* and *Anas flavirostris* were moving into bofedal and laguna habitats to breed in the wet season. For many species, occurrence in short grass increases in the dry season (Fig. 6). A possible explanation for this result would be the exploitation of a seed crop and arthropods, which presumably are seasonal as well.

Several noteworthy findings among the rarer species culled from the complete data set were documented by Gibbons *et al.* (2011), yet additional findings merit mention as they are closely associated with bofedales. Two species of conservation concern were detected several times during surveys. The White-bellied Cinclodes (*Cinclodes palliatus*) and the Diademed Sandpiper-Plover (*Phegornis mitchellii*) were assessed and listed as Critically Endangered and Near Threatened respectively by Birdlife International (2011) and the International Union for Conservation of Nature. White-bellied Cinclodes was documented in three locations: Pampa Curicocha (4800 m), a large bofedal in dpto. Junín near Marcapomacocha; Pampa de Uco (4700 m), an adjacent bofedal; and to the south in a grassier area near bofedal (4575 m) ca. 45 km WSW Huancayo, dpto. Junín. The first two sites and Ticclio, a nearby site closer to the Central highway, are where most modern records originated. Despite searching many areas historically reporting the presence of *C. palliatus*, e.g. sites in Huancavelica, no additional observations were made. It seems, given our effort in appropriate habitat within the geographic range, that this species is truly rare and restricted to the upper reaches of the puna just below snow line.

Phegornis mitchellii was observed nine times with a total of 16 individuals in dptos. Junín, Huancavelica, Arequipa, and Puno. Like *C. palliatus*, it was strongly associated with bofedales above 4500 m. These secretive plovers are much wider ranging than *C. palliatus*, extending well into central Chile and at lower elevations.

The data gathered from paired-sampling in the dry and wet seasons provides the first inter-seasonal data for species occurring in bofedales and other puna habitats. Similar to the puna's seasonal climatic character, much of the avian assemblage associated with these habitats is likewise seasonal. These results are consistent with a dynamic ecosystem supporting various life history strategies including residents, boreal and austral migrants, and heretofore unknown movement ecology that will require more focused studies to fully understand.

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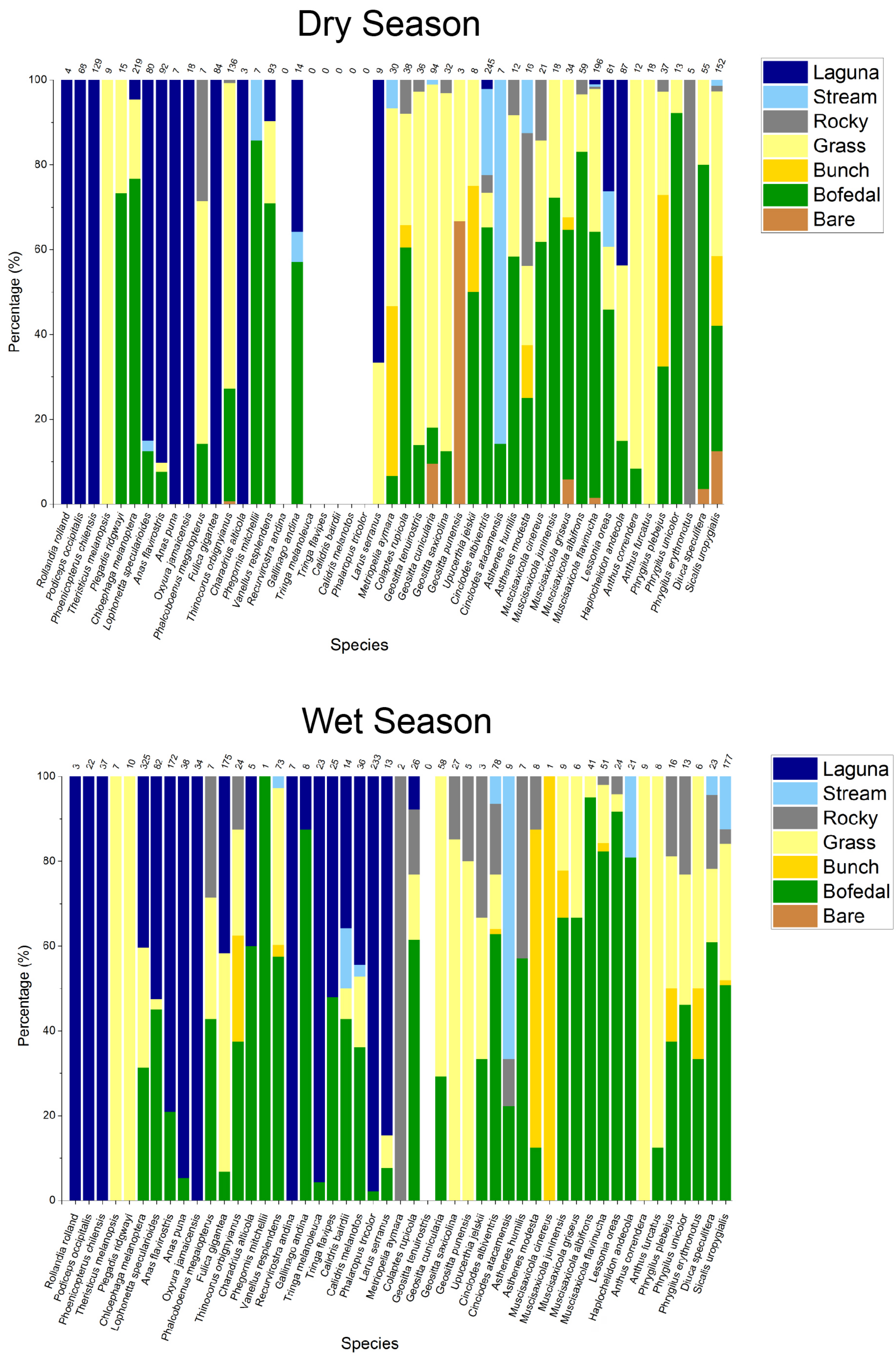

Figure 6. Species observed in the seven habitats with the number of observations for both dry and wet seasons at the top of each column. Habitats are laguna, stream, rocky, short grass (grass), bunch grass (bunch), bofedal, and bare ground (bare).

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Habitat	Bare		Bofedal		Bunch grass		Short grass		Rocky		Stream		Laguna	
Species Season	dry	wet	dry	wet	dry	wet	dry	wet	dry	wet	dry	wet	dry	wet
Rollandia rolland													4	3
Podiceps occipitalis													68	22
Nycticorax nycticorax								4				1		
Phoenicopterus chilensis													129	37
Theristicus melanopsis							9	7						
Plegadis ridgwayi			11				4	10						
Chloephaga melanoptera			168	102			41	92					10	131
Lophonetta specularioides			10	37				2			2		68	43
Anas flavirostris			7	36			2						83	136
Anas georgica													4	1
Anas puna				2									7	36
Oxyura jamaicensis													18	34
Phalcoboenus megalopterus			1	3			4	2	2	2				
Falco femoralis			1	1			1							
Fulica gigantea				12				90					84	73
Thinocorus orbignyianus	1		36	9		6	98	6	1	3				
Charadrius alticola				3									3	2
Phegornis mitchellii			6	1							1			
Vanellus resplendens			66	42		2	18	27				2	9	
Recurvirostra andina														7
Gallinago andina			8	7							1		5	1
Tringa melanoleuca				1										22
Tringa flavipes				12										13
Calidris bairdii				6				1				2		5
Calidris melanotos				13				6				1		16
Phalaropus tricolor				5										228
Larus serranus				1			3	1					6	11
Metriopelia aymara			2		12		14			2	2			
Chalcostigma olivaceum			5	1										
Oreotrochilus melanogaster			2			1								
Oreotrochilus estella				3										
Colaptes rupicola			23	16	2		10	4	3	4				2
Geositta tenuirostris			5				30		1					
Geositta cunicularia	9		8	17			76	41			1			
Geositta saxicolina			4				27	23	1	4				
Geositta punensis	2						1	4		1				
Geositta sp.				2				1						
Upucerthia jelskii			4	1	2		2	1		1				
Cinclodes albidiventris			160	49		1	20	10	10	13	50	5	5	
Cinclodes atacamensis			1	2						1	6	6		
Asthenes humilis			7	4			4		1	3				
Asthenes modesta			4	1	2	6	3		5	1	2			
Asthenes sp.			1				1	2	4					
Muscisaxicola cinereus			13			1	5		3					
Muscisaxicola juninensis			13	6		1	5	2						
Muscisaxicola frontalis			5											
Muscisaxicola griseus	2		20	4	1		11	2						
Muscisaxicola albifrons			49	39			8	2	2					
Muscisaxicola flavinucha	3		123	42		1	66	7	1	1	1		2	
Muscisaxicola capistratus							2							
Muscisaxicola sp.			7	21		1	22	2						
Agriornis montana									1	1				
Lessonia oreas			28	22			9	1		1	8		16	
Orochelidon andecola			13	17			36					4	38	

Anthus correndera			1				11	9						
Anthus furcatus				1			18	7						
Anthus sp.								8						
Zonotrichia capensis			2							1				
Phrygilus plebejus			12	6	15	2	9	5	1	3				
Phrygilus unicolor			12	6			1	4		3				
Phrygilus erythronotus				2		1		3	5					
Diuca speculifera	2		42	14			11	4		4		1		
Sicalis uropygialis	19		45	90	25	2	59	57	2	6	2	22		

Table 1. The total number of detections for each species by habitat and season.

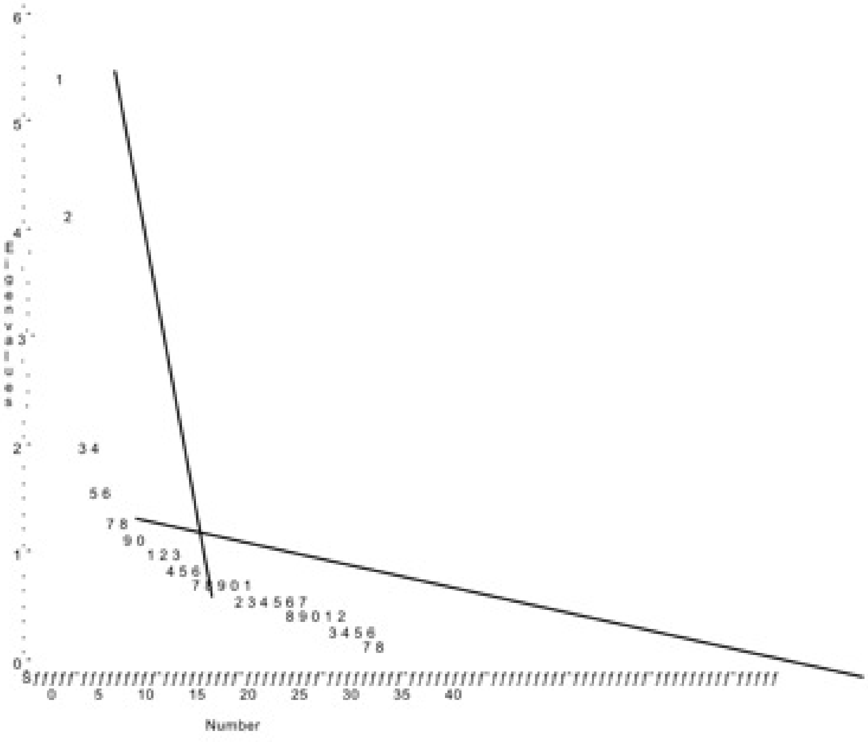
Scientific name	English name	Counts	Sum	Included
Chloephaga melanoptera	Andean Goose	81	726	Yes
Lophonetta specularioides	Crested Duck	71	301	Yes
Anas flavirostris	Yellow-billed Teal	63	522	Yes
Anas georgica	Yellow-billed Pintail	3	6	No
Anas puna	Puna Teal	17	106	Yes
Oxyura jamaicensis	Ruddy Duck	5	75	Yes
Rollandia rolland	White-tufted Grebe	6	15	No
Podiceps occipitalis	Silvery Grebe	6	98	Yes
Nycticorax nycticorax	Black-crowned Night-Heron	10	25	No
Phoenicopterus chilensis	Chilean Flamingo	11	200	No
Plegadis ridgwayi	Puna Ibis	17	104	Yes
Theristicus melanopis	Black-faced Ibis	6	20	No
Vultur gryphus	Andean Condor	1	1	No
Circus cinereus	Cinereous Harrier	1	1	No
Buteo polyosoma	Variable Hawk	6	6	No
Phalcoboenus megalopterus	Mountain Caracara	16	31	Yes
Falco femoralis	Aplomado Falcon	4	5	No
Fulica gigantea	Giant Coot	20	382	Yes
Fulica ardesiaca	Slate-colored Coot	1	1	No
Gallinula galeata	Common Gallinule	2	6	No
Vanellus resplendens	Andean Lapwing	88	294	Yes
Pluvialis dominica	American Golden-Plover	1	1	No
Charadrius alticola	Puna Plover	6	23	No
Phegornis mitchellii	Diademed Sandpiper-Plover	9	16	No
Oreopholus ruficollis	Tawny-throated Dotterel	1	3	No
Recurvirostra andina	Andean Avocet	3	15	No
Gallinago andina	Puna Snipe	29	53	Yes
Tringa flavipes	Lesser Yellowlegs	16	51	Yes
Tringa melanoleuca	Greater Yellowlegs	9	28	No
Calidris melanotos	Pectoral Sandpiper	27	98	Yes
Calidris bairdii	Baird's Sandpiper	28	175	Yes
Calidris himantopus	Stilt Sandpiper	1	12	No
Actitis macularius	Spotted Sandpiper	1	1	No
Phalaropus tricolor	Wilson's Phalarope	7	233	Yes
Thinocorus orbignyianus	Gray-breasted Seedsnipe	48	226	Yes
Chroicocephalus serranus	Andean Gull	16	34	Yes
Metriopelia melanoptera	Black-winged Ground-Dove	3	2	No
Metriopelia aymara	Golden-spotted Ground-Dove	6	32	No
Athene cunicularia	Burrowing Owl	2	3	No
Oreotrochilus estella	Andean Hillstar	3	4	No
Oreotrochilus melanogaster	Black-breasted Hillstar	4	7	No

Chalcostigma olivaceum	Olivaceous Thornbill	9	13	Yes
Colaptes rupicola	Andean Flicker	58	114	Yes
Geositta cunicularia	Common Miner	85	293	Yes
Geositta tenuirostris	Slender-billed Miner	28	60	Yes
Geositta saxicolina	Dark-winged Miner	34	126	Yes
Geositta punensis	Puna Miner	6	13	No
Geositta sp.	unidentified miner	6	10	No
Upucerthia jelskii	Plain-breasted Earthcreeper	15	19	Yes
C. albidiventris	Cream-winged Cinclodes	167	620	Yes
Cinclodes atacamensis	White-winged Cinclodes	15	23	Yes
Cinclodes palliatus	White-bellied Cinclodes	3	6	No
Leptasthenura pileata/ Leptasthenura striata	Rusty-crowned Tit-Spinetail/ Streaked Tit-Spinetail	1	1	No
Leptasthenura andicola	Andean Tit-Spinetail	2	2	No
Asthenes modesta	Cordilleran Canastero	26	44	Yes
Asthenes humilis	Streak-throated Canastero	20	35	Yes
Asthenes sp.	unidentified canastero	7	12	No
Lessonia oreas	Andean Negrito	63	191	Yes
Muscisaxicola maculirostris	Spot-billed Ground-Tyrant	1	1	No
Muscisaxicola griseus	Taczanowski's Ground-Tyrant	22	51	Yes
Muscisaxicola juninensis	Puna Ground-Tyrant	18	33	Yes
Muscisaxicola cinereus	Cinereous Ground-Tyrant	22	42	Yes
Muscisaxicola albifrons	White-fronted Ground-Tyrant	51	158	Yes
Muscisaxicola flavinucha	Ochre-naped Ground-Tyrant	114	397	Yes
Muscisaxicola rufivertex	Rufous-naped Ground-Tyrant	1	1	No
Muscisaxicola capistratus	Cinnamon-bellied Ground-Tyrant	3	4	No
Muscisaxicola frontalis	Black-fronted Ground-Tyrant	3	8	No
Agriornis montanus	Black-billed Shrike-Tyrant	3	3	No
Ochthoeca oenanthoides	d'Orbigny's Chat-Tyrant	1	2	No
Orochelidon andecola	Andean Swallow	21	129	Yes
Troglodytes aedon	House Wren	4	4	No
Anthus furcatus	Short-billed Pipit	14	36	Yes
Anthus correndera	Correndera Pipit	8	23	No
Anthus bogotensis	Paramo Pipit	2	2	No
Anthus sp.	unidentified pipit	6	14	No
Zonotrichia capensis	Rufous-capped Sparrow	14	27	Yes
Phrygilus punensis	Peruvian Sierra-Finch	1	1	No
Phrygilus unicolor	Plumbeous Sierra-Finch	20	47	Yes
Phrygilus alaudinus	Band-tailed Sierra-Finch	2	4	No
Phrygilus erythronotus	White-throated Sierra-Finch	7	16	No
Phrygilus plebejus	Ash-breasted Sierra-Finch	49	137	Yes
Diuca speculifera	White-winged Diuca-Finch	41	149	Yes
Sicalis lutea	Puna Yellow-Finch	1	2	No
Sicalis uropygialis	Bright-rumped Yellow-Finch	74	412	Yes
Carduelis magellanica	Hooded Siskin	2	4	No
Carduelis atrata	Black Siskin	2	3	No

Appendix 1. Species and number of detections for transect surveys in the wet and dry seasons of 2008 and 2009 in the high Andean puna of central and southern Peru. Rare species with less than 1% of counts or 2% of the sum were eliminated from statistical analyses.

	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6
Podiceps occipitalis	0.899	0.050	-0.098	0.004	-0.058	0.006
Oxyura jamaicensis	0.860	-0.072	-0.039	-0.016	0.074	0.009
Fulica gigantea	0.814	0.089	0.054	-0.023	-0.083	-0.011
Chroicocephalus serranus	0.769	0.063	0.049	0.158	-0.090	0.019
Phoenicopterus chilensis	0.685	0.080	0.039	-0.017	-0.100	-0.038
Phalaropus tricolor	0.571	-0.144	0.207	-0.023	0.186	-0.041
Anas puna	0.556	-0.139	0.380	-0.068	0.120	-0.008
Anas flavirostris	0.521	0.179	0.428	-0.100	-0.016	-0.036
Lophonetta specularioides	0.495	0.297	0.440	-0.072	-0.004	0.007
Cinclodes albidiventris	-0.034	0.620	-0.009	0.134	0.330	0.077
Lessonia oreas	0.096	0.577	0.265	0.126	-0.213	0.105
Muscisaxicola flavinucha	-0.019	0.576	0.021	0.319	0.191	0.109
Vanellus resplendens	0.111	0.524	0.097	0.264	0.039	-0.159
Colaptes rupicola	-0.009	0.511	-0.104	-0.063	0.196	0.233
Chloephaga melanoptera	0.237	0.480	0.315	0.235	0.208	-0.130
Orochelidon andecola	0.243	0.452	-0.145	0.340	-0.299	-0.006
Muscisaxicola juninensis	0.002	0.369	-0.038	0.028	0.058	0.070
Sicalis uropygialis	-0.023	0.362	0.021	-0.052	0.179	0.288
Gallinago andina	0.027	0.360	0.104	-0.056	0.262	-0.217
Cinclodes atacamensis	-0.023	0.358	-0.037	-0.094	-0.011	0.062
Plegadis ridgwayi	-0.003	0.319	0.191	0.294	0.120	-0.147
Calidris melanotos	0.017	0.000	0.804	0.006	-0.043	0.058
Calidris bairdii	0.022	0.061	0.725	0.057	-0.135	0.099
Tringa flavipes	0.359	-0.093	0.661	-0.041	0.093	-0.001
Anthus furcatus	-0.005	0.055	0.087	0.641	-0.111	-0.036
Geositta tenuirostris	0.001	0.036	-0.049	0.628	0.157	-0.014
Geositta saxicolina	-0.002	0.002	-0.050	0.580	0.036	-0.011
Geositta cunicularia	-0.037	0.164	0.064	0.565	-0.144	0.129
Phalcoboenus megalopterus	-0.012	-0.012	-0.026	0.321	0.119	0.011
Diuca speculifera	-0.009	0.368	-0.035	-0.041	0.606	0.010
Muscisaxicola albifrons	-0.032	0.450	0.012	-0.070	0.573	-0.141
Asthenes humilis	-0.013	-0.029	0.050	0.250	0.548	0.083
Phrygilus unicolor	0.001	0.113	-0.063	-0.047	0.491	0.011
Muscisaxicola cinereus	0.004	0.070	-0.047	0.282	0.473	0.137
Phrygilus plebejus	-0.019	0.092	0.114	-0.055	-0.022	0.662
Asthenes modesta	-0.002	0.042	-0.033	-0.073	-0.069	0.658
Thinocorus orbignyianus	-0.024	0.075	0.090	0.241	0.181	0.556
Muscisaxicola griseus	0.010	0.104	-0.035	0.350	0.303	0.391

Appendix 2. Six factors were derived from 38 species. The values (the loadings) are the correlation coefficients between the standardized original variables and the factors.



Appendix 3. This scree plot has the eigenvalues on the vertical axis and the factor indices on the horizontal axis. According to the scree plot, the amount of informative variation drops off significantly at the "elbow" of the plot. A 6-factor model was chosen for the mixed model analysis.

Laguna	Bofedal, dry season high	Bofedal,wet season high
Podiceps occipitalis	*Cinclodes albidiventris*	*Calidris melanotos*
Oxyura jamaicensis	*Lessonia oreas*	*Calidris bairdii*
Fulica gigantea	*Muscisaxicola flavinucha*	*Tringa flavipes*
Chroicocephalus serranus	*Vanellus resplendens*	*Lophonetta specularioides*
Phoenicopterus chilensis	*Colaptes rupicola*	
Phalaropus tricolor	*Chloephaga melanoptera*	
Anas puna	*Muscisaxicola juninensis*	
Anas flavirostris	*Sicalis uropygialis*	
Lophonetta specularioides	*Gallinago andina*	
	Orochelidon andecola	

Short grass, dry season high	Bofedal	Short grass, aquatic averse
Anthus furcatus	*Diuca speculifera*	*Phrygilus plebejus*
Geositta tenuirostris	*Muscisaxicola albifrons*	*Asthenes modesta*
Geositta saxicolina	*Asthenes humilis*	*Thinocorus orbignyianus*
Geositta cunicularia	*Phrygilus unicolor*	*Muscisaxicola griseus*
	Muscisaxicola cinereus	

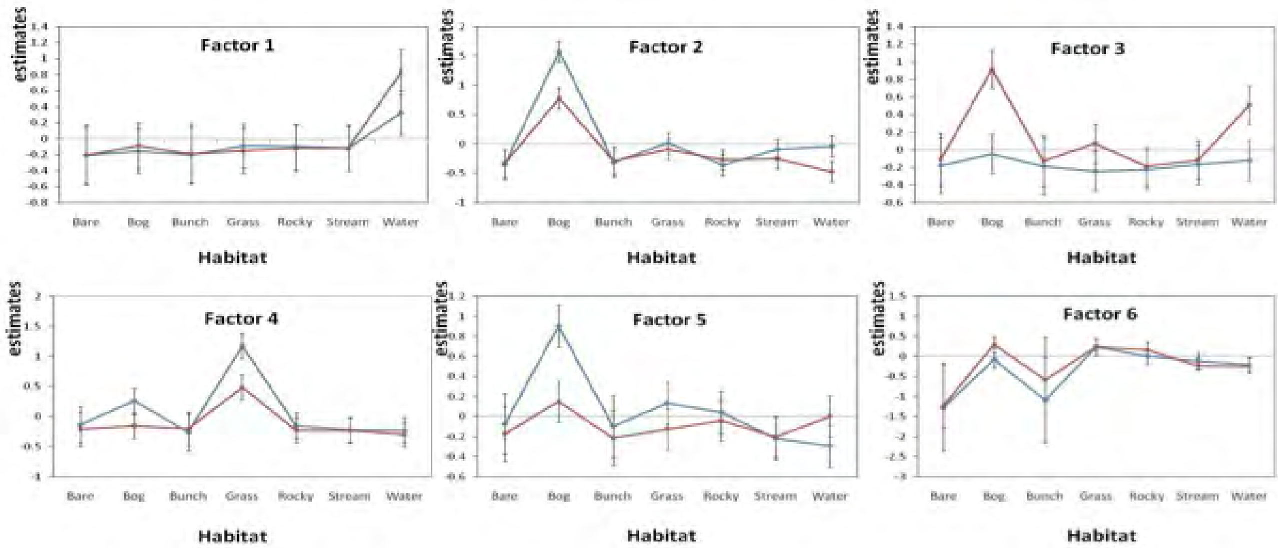
Table 2. Based on Factors from Appendix 2, six groups were derived. Species that were strongly (>.40) associated with one factor are shown.

Habitat	Factor 1		Factor 2		Factor 3		Factor 4		Factor 5		Factor 6	
Bare	-0.205	B	-0.340	B	-0.143	BC	-0.172	B	-0.124	B	-1.263	AB
Bog	-0.122	B	1.180	A	0.435	A	0.054	B	0.528	A	0.104	AB
Bunch	-0.196	B	-0.302	B	-0.156	BC	-0.232	B	-0.156	B	-0.839	AB
Grass	-0.121	B	-0.037	B	-0.087	BC	0.827	A	0.005	B	0.240	A
Rocky	-0.111	B	-0.316	B	-0.206	C	-0.190	B	0.000	B	0.082	AB
Stream	-0.122	B	-0.172	B	-0.143	BC	-0.225	B	-0.211	B	-0.175	B
Water	0.578	A	-0.256	B	0.194	AB	-0.266	B	-0.146	B	-0.232	B

Appendix 4. The effect of habitat on principal component factors are shown. For each factor, the Tukey grouping letters and the means are reported (α = 0.05). This result indicates that species related to Factor 1 preferred the open water habitat. Factors 2, 3, and 5 were associated with bofedal habitat. In addition to the positive relation to bofedal, Factor 3 had a negative association with rocky habitat. Species in the Factor 4 grouping were strongly associated with the short grass habitat. Species related to Factor 6 were also associated with short grass habitat, but had a negative association with aquatic habitats.

Season	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6
Dry	-0.0794	-0.1323	-0.1669	0.0623	0.0570	-0.2319
Wet	-0.0056	0.0630	0.1367	-0.1206	-0.0862	-0.3632
Significant	no	yes	yes	yes	no	no

Appendix 5. Effects of seasons on factors. The means for both seasons are reported. According to the results, Factor 2, Factor 3, and Factor 4 had a significant seasonality effect.



Appendix 6. Interaction graphs were constructed by plotting the estimates of means against habitat types. Red lines represent wet season, while blue lines represent dry season. The vertical bars defined by two fences indicate the range of two standard errors at each habitat type. The interaction effect was significant on Factor 2, Factor 3, Factor 4, and Factor 5.

Effects	Factor	Factor	Factor	Factor	Factor	Factor
Habitat	***	***	***	***	***	***
Season		**	***	**		
Habitat*Season		***	***	***	***	

Appendix 7. Summary table of Factor significance containing the Type 3 ANOVA test results with "***" denoting 0.001 significance, and "**" denoting 0.01 significance.