

CONSERVING BIRDLIFE OF PERUVIAN HIGHLAND BOGS: EFFECTS OF PATCH-SIZE AND HABITAT QUALITY ON SPECIES RICHNESS AND BIRD NUMBERS

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SUMMARY.—*Conserving birdlife of Peruvian highland bogs: effects of patch-size and habitat quality on species richness and bird numbers.*

Aims: Bogs (locally named “bofedales”) constitute a key habitat for conserving birds associated with the wet meadows and ponds on the huge expanses of dry bunch-grass steppes (“puna”) of the Andes. Despite this, the factors shaping bird numbers and species richness in this habitat have not been studied. This paper examines the bird communities in a set of bogs distributed in two Peruvian localities during the wet (February) and dry (September) season. It evaluates the effects of bog size and some habitat features (grazing intensity, presence of small watercourses, vegetation cover, etc.) on abundance and species richness of bird communities.

Location: Two Peruvian localities above 4,000 m (humid mountains near Cusco, and arid uplands near Arequipa).

Methods: Given that bogs tended to be long and narrow (mean width: 59 m, range 10 - 200 m), birds were counted along three parallel, simultaneous transects covering the full area of bogs. Independent variables evaluated were the size (ha), altitude (m above sea level), slope (0-90°), presence/absence of small permanent watercourses and cover (%) of water, meadows and cushion-like *Yareta* shrubs in each study bog. Grazing intensity was estimated by counting the number of faecal pellet groups (of alpacas and other livestock) inside a one-metre-wide band transect.

Results: Results support the view that bogs operate as local “hotspots” for birds, as they maintain species associated with different habitats, such as rivers and lakes (*Anas flavirostris*, *Anas specularoides*, etc.), wet meadows (*Vanellus resplendens*, *Chloephaga melanoptera*, *Cinclodes fuscus*, *Lessonia oreas*, etc.) or bunch-grass steppes (*Metriopelia aymara*, *Thinocorus orbignyianus*, etc.). Bird species richness and numbers were positively correlated with bog size and, after controlling for this effect, species richness increased in those arid upland bogs crossed by small watercourses during the dry period. This supports the key role of water availability on the bird communities of these steppes. No effect of grazing intensity and other habitat features were recorded.

Conclusions: From a conservation perspective, bog size and the presence of permanent watercourses seem to be two focal criteria for prioritizing relevant bogs for protection and can also be used as key guidelines for evaluating the pervasive effects of the reduction and alteration of bogs by public works (roads), agricultural encroachment or draining.

Key words: bogs, bird richness and abundance, bog size, conservation, grazing intensity, permanent watercourses, Peruvian Andes, puna.

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RESUMEN.—*Conservación de la avifauna de los bofedales peruanos: efectos del tamaño del bofedal y la calidad del hábitat en la riqueza de especies y en su densidad.*

Objetivos: Los bofedales constituyen un hábitat clave para la conservación de las aves asociadas a los prados húmedos y charcas de las grandes extensiones de la puna andina. Pese a ello, apenas se conocen los factores que determinan su riqueza y abundancia de aves. Este trabajo estudia las comunidades de aves en los bofedales de dos localidades peruanas durante febrero (estación húmeda) y septiembre (estación seca). En él se evalúan los efectos del tamaño del bofedal y algunos atributos del hábitat (intensidad de pastoreo, presencia de pequeños riachuelos, cobertura vegetal, etc.) sobre la riqueza y abundancia de aves.

Localidad: Dos localidades peruanas situadas por encima de los 4.000 m de altitud (las montañas húmedas próximas a Cusco y las estepas áridas de Arequipa)

Métodos: Dado que los bofedales eran largos y estrechos, las aves se estimaron a lo largo de tres transectos paralelos realizados simultáneamente de extremo a extremo de cada bofedal. Para cada bofedal se estimaron las siguientes variables de uso y estructura del hábitat: área, altitud, pendiente, presencia/ausencias de cursos de agua permanentes (arroyos), intensidad de pastoreo, y cobertura de agua, prados y arbustos de *Yareta*.

Resultados: Los resultados apoyan la idea de que los bofedales actúan como acumuladores locales de aves, dado que mantienen aves asociadas a ríos y lagos (*Anas flavirostris*, *Anas specularoides*, etc.), prados húmedos (*Vanellus resplendens*, *Chloephaga melanoptera*, *Cinclodes fuscus*, *Lessonia oreas*, etc.) y estepas de gramíneas (*Metriopelia aymara*, *Thinocorus orbignyianus*, etc.). La riqueza y abundancia de aves se asocia significativamente con el tamaño de los humedales y, en la puna más seca de Arequipa, con la presencia de arroyos. Esto sugiere el papel crítico de la disponibilidad de agua sobre las comunidades de aves de estas estepas. No se observó, sin embargo, ningún efecto de la intensidad de pastoreo u otros rasgos del hábitat.

Conclusiones: El tamaño del bofedal y la presencia de arroyos parecen ser los dos criterios esenciales a la hora de priorizar el interés conservacionista de los bofedales. Estos rasgos también pueden ser utilizados como indicadores de los efectos de la reducción y alteración de muchos bofedales por el impacto de ciertas obras públicas (carreteras), la expansión agrícola o su drenaje.

Palabras clave: Andes peruanos, bofedales, conservación, cursos de agua permanentes, intensidad de pastoreo, riqueza y abundancia de aves, puna, superficie del bofedal.

INTRODUCTION

A major part of the Andes Mountains, from Venezuela to the North of Chile and Argentina, is covered by expanses of grassland named “páramos”, “jalcas” or “punas” according to their location and climate (Cabrera, 1968; Stotz *et al.*, 1996). The highest and driest parts of these mountains and plateaus are occupied by the “puna”, a huge expanse of bunch-grass steppes (dominated by *Agrostis*, *Calamagrostis*, *Festuca*), patches of *tola*-shrubs (*Lepidophyllum*) and scattered small bogs, locally named *bofedales*, situated in upland depressions or mountain valleys. These bogs are dominated by a mixture of wet meadows (do-

minated by *Distichia muscoides*, *Alchemilla pinnata*, *Calamagrostis curvula*, etc.) frequently interspersed with cushion-like *yareta* shrubs (*Azorella yareta*, *Azorella compacta*) and small ponds and watercourses resulting from upwelling of ground water (Stotz *et al.*, 1996; Salazar, 1999; INRENA, 2001). They act as water reservoirs and, as other wetlands around the world (e.g., Whittaker and Likens, 1973), have a high primary productivity. This is why they are intensively used as pasturelands for high-quality wool producing alpacas (*Lama guanicoe pacos*), a key economical resource for local population (Flores, 1977; INRENA, 2001).

From a conservation perspective, the Andean bogs might fit the usual role of small we-

tlands in conserving local biodiversity (Gibbs, 1993). In fact, they are key habitats for conserving animals inhabiting wet meadows and ponds (e.g., amphibians, including *Bufo spinulosus*, *Pleuroderma marmorata* and *Telmatobius arequipensis*; etc.; INRENA, 2001) across the huge expanses of dry grasslands among which birds are very conspicuous elements (Venero and Brokaw, 1980; Venero, 1987; Fjelds  and Krabbe, 1990; Salazar, 1999; INRENA, 2001).

Despite the potential role of bogs as key habitats (Stotz *et al.*, 1996) in the Andean mountains and plateaus, and the well known significance for bird preservation of other wetlands in the region (e.g., salt lakes, marshes, etc.; Carbonell, 1997; Caziani *et al.*, 2001; Frazier, 2002), they have not been studied from a conservation perspective (see, however, Salazar, 1999). This may be due to the fact that they appear as scattered small patches of wet meadows across the *puna*, lacking the large concentrations of waterbirds usually considered for the selection of internationally and nationally important wetlands as Ramsar sites and Special Protection Areas (e.g., Frazier, 2002; Jackson *et al.*, 2004). However, it seems important to draw up some conservation guidelines for managing these habitat patches since they are increasingly drained, fragmented or ploughed by irrigation projects, public works or agricultural encroachment (INRENA, 1996; CONAM, 2001; *pers. obs*). In addition, and because of the role of these bogs as high quality pasturelands, it is possible that overgrazing will impair their capability for maintaining birds if livestock deplete water, pastures or affect other key environmental features (e.g., Stafford-Smith and Morton, 1990; Kruess and Tschardtke, 2002; Fondell and Ball, 2004). However, no investigations have been conducted to elucidate the main features related to the capabilities of bogs to maintain birds, despite this being an essential first step when designing management guidelines directed at conservation (Morrison *et al.*, 1998; see Fjelds ,

1988, and Fjelds  and Krabbe, 1990, for a view of the conservation problems of *puna* birds).

This paper examines the seasonal relationships between the bird numbers and species richness of bird communities and some geographical and environmental features of a sample of Peruvian highland bogs. The aims of the study were: 1) To describe the bird species using this habitat, 2) To explore the effects of the location of bogs in humid or arid *puna* (see Fjelds  and Krabbe 1990) on the structure of bird communities, 3) To test the role of bog area on bird numbers and species richness given that size is a main determinant of the number of species and individuals occupying a habitat patch (Rosenzweig, 1995; see however Oertli *et al.*; 2002) and 4) To evaluate the role of habitat quality on bird communities (see Wiens, 1989, for a review); more specifically, the effects of habitat structure, grazing intensity and the presence of small stable watercourses across the bogs, a fair indicator of permanent water availability.

MATERIAL AND METHODS

Study area

Two groups of highland bogs were studied. Mountain bogs were sampled at the Lares and Amparaes passes (13° 12'S, 71° 54'W; altitudinal range: 3,920 - 4,800 m), two pasturelands located in the mountain range between the Valley of the Incas (Calca, Department of Cusco) and Peruvian Amazonia (Manu). Upland bogs were also sampled on the plains of the National Reserve of Salinas-Aguada Blanca (16° 15'S, 71° 21'W, altitudinal range: 3,750 - 4,220 m, Department of Arequipa; Fig. 1). These two localities differ dramatically in rainfall, as is well illustrated by comparing the annual precipitations of two nearby cities (Cusco: 671.2 mm and Arequipa: 99.6 mm; data bank: World Climate© 2005, www.worldclimate.com). The study was con-

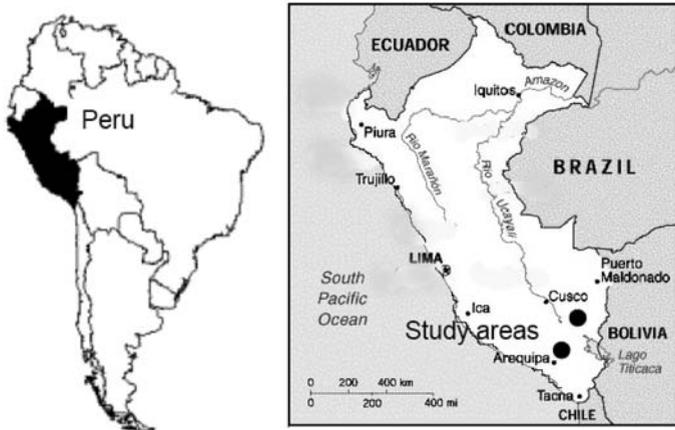


FIG. 1.—Location of the study areas in Peru.
[Localización de las áreas de estudio.]

ducted in September 2002 (dry season; mean precipitations: 23.7 mm in Cusco and 0.4 mm in Arequipa) and February 2003 (wet season; mean precipitations: 115.0 mm in Cusco and 41.5 mm in Arequipa) to evaluate the seasonal capability of bogs for maintaining birds. It is interesting to note that many highland bird species breed in the wet season (Fjeldså and Krabbe, 1990). Sixteen mountain bogs (totalling 29 ha) and 14 upland bogs (47.6 ha) were studied. The largest *bofedales* of the last area (e.g. Toccca; see Salazar, 1999) were excluded because of the extreme difficulty to record their complete bird communities, particularly the numbers of small passerines occupying the bog. The study bogs were georeferenced in September by means of a GPS device to relocate them easily during the February counts.

Bird counts, habitat features and analyses

Bird species and individuals were recorded in each study bog. All species were included since the aim was to assess the use (for nesting, watering, feeding, etc.) of bogs by the

whole bird community of the study areas. Given that bogs tended to be long and narrow (mean width: 59 m, range 10 - 200 m), the three authors counted co-ordinately and simultaneously all the birds recorded along three parallel transects, distributed along the longer axis, covering the full area of bogs. The size (ha), altitude (m above sea level), slope (0-90°) and cover (%) of water, meadows and cushion-like *Yareta*-shrubs were evaluated in each study bog by using GPS devices and visual estimation (see Prodon and Lebreton 1981). Other variables recorded were the presence/absence of small permanent watercourses across bogs and the number of faecal pellet groups of alpacas (predominant), horses, cattle, sheep and pigs inside a one-metre-wide band in a transect along the bog. Grazing intensity was expressed as the mean number of pellet groups/100m.

General Linear Models (GLM) were used for analyzing the main effects of the environmental features considered in this study on bird abundance and richness (see GLM module of Statistica 6.1; StatSoft, 2002). Mean scores of the two counts were used for evaluating the factors affecting bird communities in order to work with more sound bird data for assessing the

TABLE 1

Main environmental features (mean \pm SE) of the mountain (Lares and Amparaes passes) and upland (National Reserve of Salinas-Aguada Blanca) bogs studied and tests for differences between mountain and upland bogs.

[Principales rasgos ambientales (media \pm SE) de los bofedales estudiados en los Andes (izquierda: bofedales de montaña, puertos de Lares y Amparaes) y en la puna (derecha: Reserva Nacional de Salinas-Aguada Blanca).]

	Mountain bogs (n = 16)	Upland bogs (n = 14)	F _{1,28}	P
Altitude (m)	4,325.6 \pm 42.2	4,138.6 \pm 45.1	9.00	0.006
Slope (degrees)	8.06 \pm 1.93	6.71 \pm 2.07	0.01	0.916
Yareta shrubs (% cover)	50.81 \pm 6.51	40.18 \pm 7.00	1.39	0.248
Meadow (% cover)	37.06 \pm 6.35	52.29 \pm 6.78	2.50	0.125
Water (% cover)	9.41 \pm 2.73	7.54 \pm 2.92	0.09	0.760
Area (ha)	1.85 \pm 0.99	3.40 \pm 1.06	1.05	0.315
Livestock (n° faecal pellets/100m)	9.70 \pm 1.13	7.80 \pm 1.21	1.27	0.270

conservation interest of bogs and to avoid the effects of over-parameterization. However, separate data from dry and rainy periods were also used for exploring some seasonal changes in the structure of bird communities. In addition, in order to reduce the number of some parameters related to habitat features a Principal Component Analysis (PCA) on vegetation cover (mean scores of the two periods), altitude and slope was conducted. Only the first component (PC1; eigenvalue: 2.26, explained variance: 45.27 %) was selected; PC1 represented a gradient from higher bogs, with high cover of *Yareta* shrubs, to lower bogs with high cover of meadows (altitude: 0.628, slope: 0.206, *Yareta* shrub cover: 0.908, meadow cover: -0.925, water cover: 0.384). Variables were log and arcsine (covers) transformed to meet normality requirements.

RESULTS

Features of the study bogs

Mountain and upland bogs had a similar structure, but differed in altitude (Table 1). In

fact, they hardly differed in mean factor scores along the PC1 despite mountain bogs being higher and having more *Yareta* shrubs than upland bogs (mean factor scores \pm SE; mountain bogs: 0.49 \pm 0.36; upland bogs: -0.56 \pm 0.38; $F_{1,28}=3.97$, $P=0.056$). During the rainy period (February) there was a small albeit significant increase in water cover (from 7.4 % to 9.7 %; repeated measures GLM: $F_{1,28}=10.55$, $P=0.003$) and a decrease (through flooding) of meadows (from 45.5 % to 42.8 %; repeated measures GLM: $F_{1,28}=8.51$, $P=0.007$). Cover of *Yareta* shrubs did not vary between seasons (45.9 % to 45.8 %; $F_{1,28}=0.16$, $P=0.694$).

Species richness

The bird communities that used bogs as breeding, feeding or watering sites seemed to be composed by three main groups of species according to their habitat preferences (Appendix): lakes and rivers (e.g., *Anas flavirostris*, *Anas specularoides*, etc.), wet meadows (*Vanellus resplendens*, *Chloephaga melanoptera*, *Cinclodes fuscus*, *Lessonia oreas*, *Muscisaxi-*

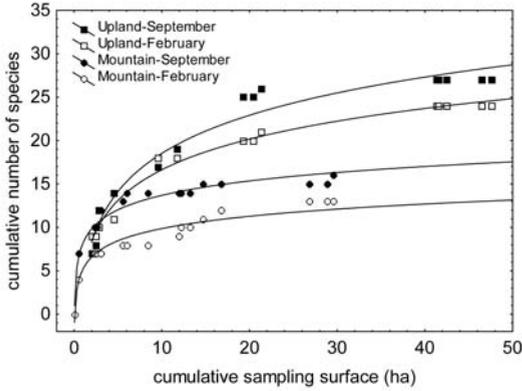


FIG. 2.—Cumulative number of bird species recorded in mountain and upland bogs according to the cumulative surface sampled in the study bogs (29.0 and 47.6 ha in mountain and upland bogs respectively).

[Número acumulado de especies de aves registradas en los bofedales de montaña y de puna en función del área acumulada muestreada en los bofedales estudiados (29,0 ha y 47,6 ha, respectivamente).]

cola alpina, etc.) and bunch-grass steppes (*Metriopelia aymara*, *Thinocorus orbignyianus*, *Phrygilus plebejus*, *Sicalis uropygialis*, etc).

The cumulative number of bird species recorded in bogs was rather similar in the two

periods, despite sharp differences between mountain and upland bogs, with nearly twice as many species recorded in the latter (Fig. 2; Appendix). However, these differences in the total number of species occurring in mountain and upland bogs were not detected when analyzing the number of species per bog (Fig. 3; repeated measures GLM; locality: $F_{1,28} = 2.65$, $P = 0.115$; season: $F_{1,28} = 0.388$, $P = 0.538$; locality x season interaction: $F_{1,28} = 1.462$, $P = 0.237$).

Bog size was the single determinant of the mean number of bird species occurring in bogs (Table 2; Fig 4). There was, however, a significant interaction between locality and the presence of permanent watercourses (Table 2), suggesting a different effect of the presence of watercourses on species diversity in mountain and upland bogs during the dry (September) and rainy (February) periods. Results showed that, after controlling for the effect of bog size, the presence of watercourses affected the number of species positively in upland bogs during the dry (September) and rainy (February) periods. This result was explored by analyzing the effects of the presence of watercourses on the species richness of upland and mountain bogs during the dry (September) and rainy (February) periods. Results showed that, after controlling for the effect of bog size, the presence of watercourses affected the number of species positively in upland bogs during the dry (September) and rainy (February) periods. This result was explored by analyzing the effects of the presence of watercourses on the species richness of upland and mountain bogs during the dry (September) and rainy (February) periods.

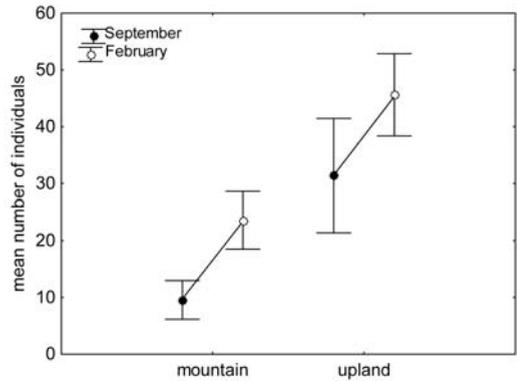
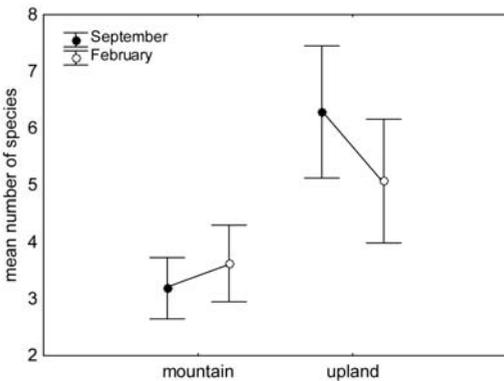


FIG. 3.—Seasonal changes in the mean numbers (\pm SE) of species and individuals occurring in mountain and upland bogs.

[Variación estacional del número medio (\pm SE) de especies e individuos registrados en los bofedales alpinos (montaña) y de puna.]

TABLE 2

Results of mixed General Linear Models analyzing species richness and bird numbers in function of bog area, livestock abundance and habitat structure (PC1, see text), controlling for variation between locality (mountain vs. upland) and presence/absence of watercourses.

[Resultados de los GLM realizados para analizar los efectos del área del bofedal, la intensidad de pastoreo y la estructura del hábitat (PC1) sobre la riqueza y la abundancia de aves en los bofedales, controlando el efecto de la localidad (montaña vs puna) y de la presencia/ausencia de cursos de agua permanentes.]

	Species richness			Bird numbers		
	$F_{1,23}$	P	beta	$F_{1,23}$	P	beta
Area	1.81	0.003	0.466	17.49	< 0.001	0.549
Livestock	3.67	0.068	0.265	1.40	0.249	0.152
Habitat (PC1)	0.61	0.442	0.144	0.21	0.652	0.078
Locality	1.82	0.191		8.43	0.008	
Watercourse	2.05	0.166		0.56	0.464	
Locality x Watercourse	5.62	0.027		1.43	0.243	
Model	$F_{6,23}=6.20$ < 0.001 $R^2=0.62$			$F_{6,23}=7.86$ < 0.001 $R^2=0.67$		

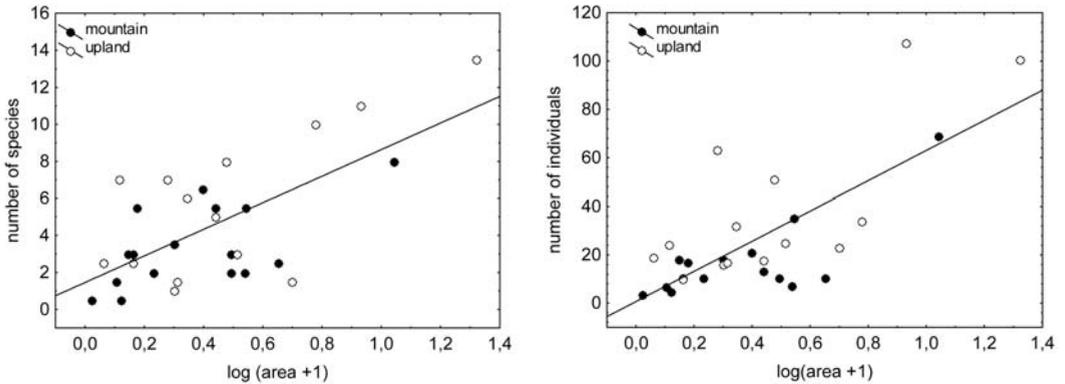


FIG. 4.—Relationships between bog size and the number of species and individuals.

[Relaciones entre el área del bofedal y el número de especies e individuos.]

$F_{1,25} = 5.92, P = 0.022$; watercourse x location interaction: $F_{1,25} = 4.82, P = 0.038$). However, in the rainy period no significant effect of watercourses on species richness was observed (watercourse: $F_{1,25} = 1.73, P = 0.200$; watercourse x location interaction: $F_{1,25} = 2.33, P = 0.139$).

Bird numbers

Bird numbers were higher in upland bogs, a trait that increased from the dry to the wet period (Fig. 3; locality: $F_{1,28} = 7.92, P = 0.009$; season: $F_{1,28} = 2.54, P < 0.001$; locality x season interaction: $F_{1,28} = 0.06, P = 0.804$). Mean

number of birds in bogs was strongly correlated with bog size (Table 2, Fig.4). As in the case of species richness, the potential role of watercourses on bird abundance in dry and wet periods was also investigated. Watercourse presence was positively related to the number of birds in upland bogs during the dry period (Fig. 5; effect of watercourse: $F_{1,25} = 6.80$, $P = 0.015$; watercourse x location interaction: $F_{1,25} = 4.25$, $P = 0.049$), but not during the wet period (effect of watercourse: $F_{1,25} = 0.04$, $P = 0.847$; watercourse x location interaction: $F_{1,25} = 0.91$, $P = 0.350$).

DISCUSSION

Species composition

Results support the view that bogs operate as local “hotspots” for birds, as they maintain species associated with different habitats, such as rivers and lakes, wet meadows or bunch-grass steppes. This suggests that bogs, in addition to their role as suitable sites for some bird species (e.g., those related to moist habitats), draw birds from the surrounding dry grasslands.

The bird communities of upland and mountain bogs differed in the total number of species, with upland bogs having a larger number of species than the mountain ones (Fig. 2). In fact, mountain bogs seemed to be occupied by a sub-sample of upland birds (excluding isolated records of two species, *Carduelis magellanica* and *Muscisaxicola macloviana*; Appendix). This pattern can be related to the absence from the Lares and Amparaes passes (Cusco) of some individual species (e.g., *Lessonia oreas* and *Thinocorus orbignyianus*) common at Salinas-Aguada Blanca (Arequipa). However, it can also result from differences in the size of bogs: upland bogs were larger and thus held more species (Fig. 4). In fact, the largest upland bogs considered in this study attracted some waterbird species absent from mountain

bogs (e.g., *Plegadis ridgwayi*, *Recurvirostra andina*, *Gallinago andina*, *Calidris bairdii* and *Charadrius alticola*). This interpretation is supported by the fact that there was no effect of locality on species richness (Table 2), after controlling for the effect of bog size.

Seasonal changes

The species composition of bird communities changed slightly between seasons. In some cases, it seemed to be related to altitudinal movements of birds coming from lower areas, as in the case of rufous-collared sparrow (*Zonotrichia capensis*), which was recorded as breeder in these highland bogs during the wet season (Appendix). In other, these changes could be related to long-distance latitudinal migrations, as with some North American waders (*Calidris bairdii*) or some ground-tyrants (*Muscisaxicola albilora*, *Muscisaxicola macloviana*; Fjeldså and Krabbe, 1990; Clements and Shany, 2001). However, despite these minor differences, it is interesting to emphasize the similarity in community structure across the seasonal cycle (see Appendix), a constancy supported by the lack of significant changes in the mean number of species occurring in bogs during the two seasons (Fig. 3).

There was, however, a seasonal change in the mean number of individuals occurring in bogs (Fig. 3). This pattern is probably related to the breeding cycle of the Andean avifauna, as bogs had higher numbers of birds in February at the end of the breeding period. This could explain, for instance, the large numbers of “finches” (*Phrygilus plebejus*, *Sicalis uropygialis*) occurring in this habitat during this period. Other species, however, did not fit to this pattern as they decreased during the breeding period. This is the case, for instance, of seedsnipes (*Thinocorus orbignyianus*) and ground-doves (*Metriopelia aymara*) that left massively the upland bogs during the breeding period, probably for breeding in

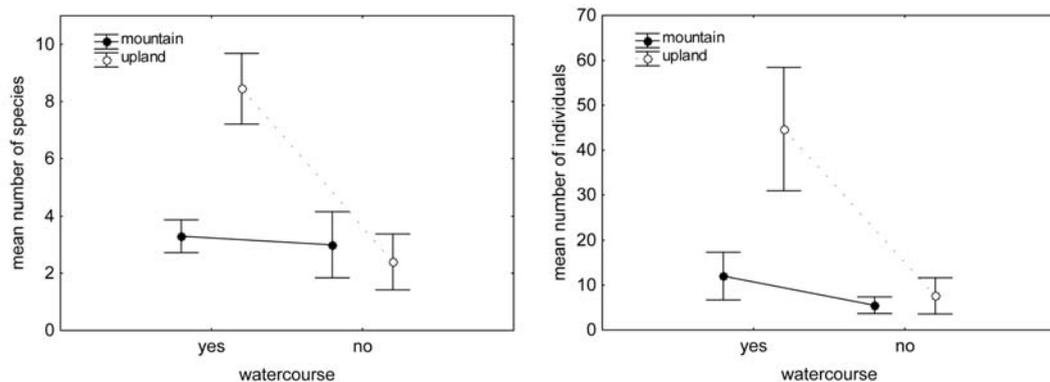


FIG. 5.—Changes in the mean number (\pm SE) of species and individuals occurring in mountain and upland bogs during the dry season according to the presence of watercourses.

[Variación del número medio (\pm SE) de especies e individuos registrados en los bofedales de montaña y de puna durante la estación seca en función de la presencia de cursos de agua permanentes.]

higher areas (Fjeldså and Krabbe, 1990). In other cases, this seemed to be related to seasonal variations in habitat preferences, as in the Andean goose (*Chloephaga melanoleuca*) that leaves bogs to occupy hills or rocky slopes during the breeding period (Fjeldså and Krabbe, 1990). This suggests that changes in the use of bogs by birds inhabiting the Peruvian highlands are not synchronous at all and depend strongly on the particular seasonal requirements of individual species.

Factors affecting bird communities in bogs

Bog area was the main predictor of species richness, a common rule in nature (Rosenzweig, 1995) that clearly applies to birds and other organisms inhabiting lakes and marshlands (Hobæk *et al.*, 2002; Paracuellos and Tellería, 2004; but see Oertli *et al.*, 2002). As we have stressed before, the larger size of some bogs in uplands (Fig. 4) could explain the presence of some additional species and thus the observed differences with mountain bogs (Fig. 2). However there was also an additional effect of the presence of permanent watercourses (Table 2). This was particularly clear in the uplands

of Salinas-Aguada Blanca during the dry season (Fig. 5), a finding that suggests the main effect of permanent running water across bogs on birds in the *arid puna*. These small watercourses guarantee drinking sites for steppe birds and must be considered as the main habitat for some species (e.g., *Cinclodes fuscus* and *Cinclodes atacamensis*). In addition, streams running through bogs during the stressing dry season are a fair indicator of permanent water availability for birds and of continued primary productivity of wet meadows - suitable for many species (see Appendix) - particularly in the dry bunch-grass steppes of Salinas-Aguada Blanca. This agrees with the observed relationships between species richness and productivity, with richness increasing from low to intermediate productivity levels (Rosenzweig, 1995; Waide *et al.*, 1999).

Bird abundance, as determined by the total number of individuals occurring in bogs, was also strongly determined by bog size, larger bogs attracting more individuals (see Caziani *et al.*, 2001, for similar results from Argentine upland wetlands). However, abundance was also affected by the geographical location of bogs. Upland bogs, other factors being equal, held larger numbers of birds than mountain ones. This could

also be explained by the capacity of these highly productive wet habitat patches for collecting birds from the surrounding arid *puna*, especially during the dry season (Fig. 5).

Conclusions

It has been commented that, whereas the *puna* seems quite uniform on casual observation, it is sufficiently complex structurally to restrict the distribution of many birds, giving a patchy distribution of species (Vuilleumier and Simberloff 1980). In fact, most birds adapted to open spaces are patchily distributed within the *puna* because they seem to be restricted by the effects of local habitat gradients (Fjeldså and Krabbe, 1990). This means that, taking into account their ability for attracting birds, bogs interspersed in the dry bunch grass steppes will probably be one of the main shapers of the spatial patterning of bird species distribution in the *puna*. Consequently, and despite most *puna* birds seeming currently to maintain good populations (Fjeldså, 1988; Fjeldså and Krabbe, 1990; but see Stattersfied and Capper, 2000), it seems important to preserve the functional role of bogs to preserve Andean bird life. Thus, in addition to the protection of important key areas for birds in the *puna* region (e.g., Wege and Long, 1995; Frazier, 2002), it is important to produce some management guidelines directed at improving the conservation of bogs (and other key habitats; e.g. *tola*-shrub patches) across the deforested huge spread of the Andes.

Effects on species richness, a focal parameter in conservation (e.g., Williams *et al.*, 1998), are usually determined by interdependent processes operating at local scales, such as the reduction of habitat patch sizes and the pervasive interference of some human activities on habitat quality (Harrison and Bruna, 1999). It has been pointed out that bog size is a main determinant of bird species diversity and that, other factors being equal, the ability of bogs to

retain bird species is related to the availability of small watercourses running through wet meadows in arid *puna*. Results in this study also support the lack of negative incidence of domestic animals on birds, at least in the range of livestock abundance we have recorded in the study areas. This is a promising result that needs further investigation, particularly in large periods of widespread drought when the dependence of wildlife on these productive patches can be strongly affected by the grazing intensity of domestic livestock (Stafford-Smith and Morton, 1990).

From this follows two basic considerations for detecting and prioritizing relevant bogs for conservation: larger bogs across the Peruvian highlands, and bogs crossed by small watercourses in the drier sectors, hold the largest number of bird species. These two basic findings may also be useful for predicting the pervasive effects on birdlife of some current processes of bog size reduction and fragmentation by public works and agricultural encroachment, or the negative impact of the draining of bogs as an indirect consequence of the alteration of some water catchments to improve irrigation projects in lowland, arid regions of coastal Peru (INRENA, 1996).

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APPENDIX [APÉNDICE]

Bird densities ($n^{\circ}/10$ ha) in mountain and upland bogs obtained by dividing the cumulative number of individuals recorded during the censuses by the cumulative area sampled in each bog type. Species are classified according to their main habitat preferences, following Fjeldså and Krabbe (1990) and *pers. obs.* (M: meadows, S: steppes, W: waters).

[Densidades de aves (n° individuos/10 ha) en los bofedales de montaña (izquierda, localidades andinas) y de puna (derecha). La clasificación de las especies, en función de sus preferencias de hábitat, está basada en Fjeldså and Krabbe (1990) y en *obs. pers.* (M: prados, S: estepas, W: humedales).]

		Mountain (29.0 ha)		Upland (47.6 ha)	
		September	February	September	February
<i>Chloephaga melanoptera</i>	M	1.03	-	15.56	5.68
<i>Anas specularoides</i>	W	0.69	-	1.05	0.42
<i>Anas flavirostris</i>	W	1.38	0.69	1.47	4.84
<i>Plegadis ridgwayi</i>	W	-	-	-	0.63
<i>Phalacrocorax megalopterus</i>	M	1.03	+	1.26	-
<i>Gallinago andina</i>	W	-	-	0.21	0.21
<i>Recurvirostra andina</i>	W	-	-	0.42	-
<i>Calidris bairdii</i>	W	-	-	-	6.31
<i>Charadrius alticola</i>	W	-	-	0.42	0.21
<i>Vanellus resplendens</i>	M	-	-	2.73	1.68
<i>Thinocorus orbignyianus</i>	S	-	-	20.19	2.94
<i>Larus serranus</i>	W	-	0.34	0.21	-
<i>Metriopelia ayмара</i>	S	-	-	14.51	0.84
<i>Colaptes rupicola</i>	S	0.34	1.38	0.84	-
<i>Oreotrochilus estella</i>	S	-	-	-	0.21
<i>Asthenes modesta</i>	S	-	0.69	0.21	0.42
<i>Geositta cunicularia</i>	S	1.72	0.69	4.84	2.31
<i>Geositta crassirostris</i>	S	-	-	0.21	-
<i>Cinclodes fuscus</i>	M	14.14	17.25	8.83	6.94
<i>Cinclodes atacamensis</i>	M	0.34	0.34	0.42	0.21
<i>Lessonia oreas</i>	M	-	-	5.47	4.84
<i>Muscisaxicola albifrons</i>	M	-	-	0.21	0.21
<i>Muscisaxicola maculirostris</i>	M	-	-	-	0.42
<i>Muscisaxicola alpina</i>	M	5.86	3.79	6.31	0.42
<i>Muscisaxicola flavinucha</i>	M	-	-	1.26	0.63
<i>Muscisaxicola albilora</i>	M	-	-	0.34	-
<i>Muscisaxicola macloviana</i>	M	0.34	-	-	-
<i>Phrygilus unicolor</i>	S	7.93	6.90	0.42	-
<i>Phrygilus plebejus</i>	S	3.10	3.79	1.26	19.14
<i>Carduelis magellanica</i>	S	0.34	+	-	-
<i>Carduelis atrata</i>	S	-	-	-	0.63
<i>Sicalis uropygialis</i>	S	6.90	30.70	2.10	9.67
<i>Diuca speculifera</i>	M	5.17	11.38	0.84	0.42
<i>Zonotrichia capensis</i>	S	-	2.76	-	1.89