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ECO-CLIMATIC CORRELATES OF OCCURRENCES OF WHITE-THROATED HAWK (*BUTEO ALBIGULA*) AND CINEREOUS HARRIER (*CIRCUS CINEROUS*) IN CENTRAL ECUADOR

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Resumen. – **Correlaciones eco-climáticas de ocurrencias del Aguilucho andino (*Buteo albigula*) y del Aguilucho cenizo (*Circus cinereus*) en el centro del Ecuador. –** El Aguilucho andino (*Buteo albigula*) y el Aguilucho cenizo (*Circus cinereus*) son rapaces escasos en los Andes del Norte. En 2004, cada especie fue observada respectivamente 16 y 7 veces durante el monitoreo de 197 sitios en los Andes centrales del Ecuador. Modelando datos de presencia-ausencia, caracterizamos sus nicho climático, hábitat y área potencial de distribución. Presentamos los primeros registros del Aguilucho andino en el centro del Ecuador. El aumento mensual de la frecuencia de observación sugiere un origen migratorio. Todos los individuos fueron observados en zonas agrícolas abiertas con bosques dispersos de eucaliptos, correspondiendo a la cobertura de suelo 'matorral y pastizal', un hábitat inusual para la especie. La presencia de la especie estuvo principalmente relacionada con la elevación con un óptimo entre 3080 y 3350 m, y temperaturas moderadas (7.6–14.2°C). El Aguilucho cenizo fue escaso, y su presencia se relacionó principalmente con precipitaciones bajas (63–82 mm por mes). Los modelos de distribución sugieren que las dos especies podrían existir a todo lo largo de los Andes ecuatorianos, pese a la predicción que el Aguilucho cenizo esta ausente localmente en el valle interandino central.

Abstract. – During a 2004 survey of 197 sites in the central Andes of Ecuador, we observed two rare raptors, the White-throated Hawk (*Buteo albigula*) and Cinereous Harrier (*Circus cinereus*), 16 and seven times respectively. Their climatic niche, habitat, and potential distribution range were characterized with presence-absence modeling. Occurrence of the White-throated Hawk is reported for the first time for central Ecuador. The seasonal increase in frequency of occurrence suggests northward post-nuptial migration in this species. All individuals were observed in open, agricultural lands with scattered stands of *Eucalyptus* trees, an unusual habitat for the species. Presence was mainly associated with an optimal elevation range between 2680 and 3550 m and moderate temperatures (7.6–14.2°C). The Cinereous Harrier was rare, and its presence was mainly associated with areas of low precipitation (63–82 mm per month). Distribution models suggest that both species could occur continuously all along the Ecuadorian Andes, although Cinereous Harrier is predicted to be locally absent in the central inter-Andean valley. *Accepted 26 August 2009.*

Key words: Cinereous Harrier, White-throated Hawk, climatic correlates, distribution, ecological niche model, *Eucalyptus*, habitat, predicted distribution, South America.

INTRODUCTION

The White-throated Hawk (*Buteo albigula*) and Cinereous Harrier (*Circus cinereus*) are widely distributed raptors in the Neotropics, both ranging from Venezuela to Chile and Argentina (Fig. 1; Fjeldså & Krabbe 1990, Ridgely *et al.* 2003). However, the White-throated Hawk is consistently rare in both its breeding (temperate rainforest in Chile and Argentina; Krabbe *et al.* 1998, Jaksic *et al.* 2001, Figueroa Rojas *et al.* 2002, Trejo *et al.* 2007, Silva-Rodríguez *et al.* 2008) and wintering grounds (central and northern Andes; Fjeldså & Krabbe 1990, Ridgely & Greenfield 2001, Restall *et al.* 2006, Schulenberg *et al.* 2007, Trejo *et al.* 2007). The Cinereous Harrier is locally uncommon to rare in the Andes of Ecuador (Ridgely & Greenfield 2001) and southern Colombia (Fjeldså & Krabbe 1990); its status is uncertain in central and northern Colombia (Fjeldså & Krabbe 1990, Restall *et al.* 2006) whereas it is locally common south of Ecuador (Jimenez & Jaksic 1988, Fjeldså & Krabbe 1990, Schulenberg *et al.* 2007). As a consequence of the overall scarcity of both species, their biology is still poorly described, particularly for the White-throated Hawk (Figueroa Rojas *et al.* 2002), and quantitative data on environmental determinants of their occurrence are scarce.

Modeling of presence-absence data is becoming a major tool to extract objective characterizations of the habitat requirements, ecological niches, and potential distributional range of species from basic records of presence-absence (Rotenberry *et al.* 2006, Raxworthy *et al.* 2007). This statistical tool is particularly powerful to acquire robust knowledge on the natural history of rare species, e.g., poorly detectable, inconspicuous, low density species, or species dwelling in remote, poorly investigated habitats (Engler *et al.* 2004, Guisan *et al.* 2006). Recently, new algorithms, relying on maximum entropy (MAXENT; Phillips *et al.* 2006) or classification procedures (e.g., Mahalanobis classification; Rotenberry *et al.* 2006) have been used to model presence only data. The MAXENT model is particularly well suited to model non-linear responses of species to their environments. Straight-line relationships corresponding to linear gradients are sometimes observed, but non-linear responses are generally expected (Austin 2007). For example, habitat suitability could reach an optimum level for a particular value of an eco-climatic variable, and could decrease towards the periphery with a specific ecological amplitude (Coudun & Gégout 2005). However, adding absence data allows a better niche definition and improves model accuracy (Engler *et al.* 2004). In that case, Generalized Additive Models (GAMs) can be used to analyze presence-absence data because of their ability to model non-linear relationships (Austin 2002). They provide better fits and more accurate niche-based species distribution models than Generalized Linear Models (Randin *et al.* 2006).

Being aware of the scarcity of White-throated Hawk and Cinereous Harrier, we systematically recorded all opportunistic observations of these species (Table 1) during an ornithological research project led in the provinces of Cotopaxi, Chimborazo, and Tungurahua, central Ecuador, in 2004. Our aim was to identify the major determinants of their eco-climatic niches in the study area and to compare them with available descriptions of their habitat requirements. Firstly, we identify eco-climatic features that significantly correlate with the presence-absence of each species in our study area. Secondly, we present spatial predictions of potential distribution range in the Ecuadorian Andes for both species.

METHODS

Presence-absence of the White-throated Hawk and the Cinereous Harrier were recorded in the inter-Andean valleys of central Ecuador (78°28'–78°46'W, 0°55'–1°56'S) between the towns of Latacunga (Cotopaxi Province) to the north and Guamote (Chimborazo Province) to the south mainly in the altitudinal range 2300–3700 m. This altitudinal range actually encompasses most of the known altitudinal range for both species in Ecuador (see below).

Data were collected opportunistically during an intensive 105-day field survey conducted in March–July 2004. The survey consisted in the continuous, transect or point, monitoring of radio-tagged House Sparrows (*Passer domesticus*), from 06:00–18:00 h, at a total of 194 locations. Geographical coordinates and altitude (± 50 m) of each location were taken with a GPS. All opportunistic observations of rare species were systematically recorded. Non-detection of species was considered as absence if the point count duration was at least 10 min. To minimize pseudoreplication, records less than 1 km apart were pooled prior to the analyses. The final matrix comprised 335 1-km^2 cells located on a study area covering approximately 5000 km^2.

Eco-climatic variables most likely to explain the presence of each species (Table 2) were derived from habitat and range descriptions available in the literature. Values for candidate eco-climatic variables to be used as predictors of species presence were obtained as follows. Land-cover information was extracted from GLC (2003; 1 km^2 resolution). Land cover type was reclassified in three habitat classes: shrub and herbaceous cover, forest, or cropland. This classification corresponded to the landscape divisions observed in our study area. We also tested for an effect of the percentage of forested area in a 10-km radius circle centered on each sampling site, the distance to the nearest stream or lake (km), and the human population density (inhabitants/km^2). A 30-m resolution digital elevation model (Instituto Geográfico Militar) was used to compute a mean cell elevation and to derive slope (in %) and aspect (slope orientation in degrees). Climatic variables were extracted from WorldClim V1.4. (Hijmans *et al.* 2005). We included the annual mean monthly temperature (°C) and precipitation (mm) and an aridity index defined as the ratio between precipitation and temperature (mm/°C).

Species eco-climatic niches were defined as the combination of responses along single environmental gradients. Identification of eco-climatic correlates and estimates of probability of presence for each species per pixel (1 km^2) were obtained with Generalized Additive Models (SAS V9), assuming a binomial distribution for presence-absence data with a logit link function (Hastie & Tibshirani 1990). Landscape variables were fitted separately using a univariate smoothing spline with two or three degrees of freedom to test for linear (gradient) or quadratic (optimum range, quantified by 95% confidence interval) relationships. Univariate models allowed us to characterize the distribution of species along each ecological gradient. The significance of variables was tested with χ^2-statistics computed as the difference in deviance between the null model and the model containing the explanatory variable. A probability of presence was calculated for each pixel and for each landscape variable. The contribution of each variable to the spatial prediction was quantified by the Akaike weight (*Wi*, Burnham & Anderson 1998). The final model used to predict the probability of presence of each species over the whole area included all landscape variables that had a significant effect. The final probability of presence was obtained by weighting with *Wi* the probability estimates obtained for each landscape variable. Only those landscape variables that had a significant effect were used. By this simple method, we avoided the problem of biased parameter estimates due to multicolinearity

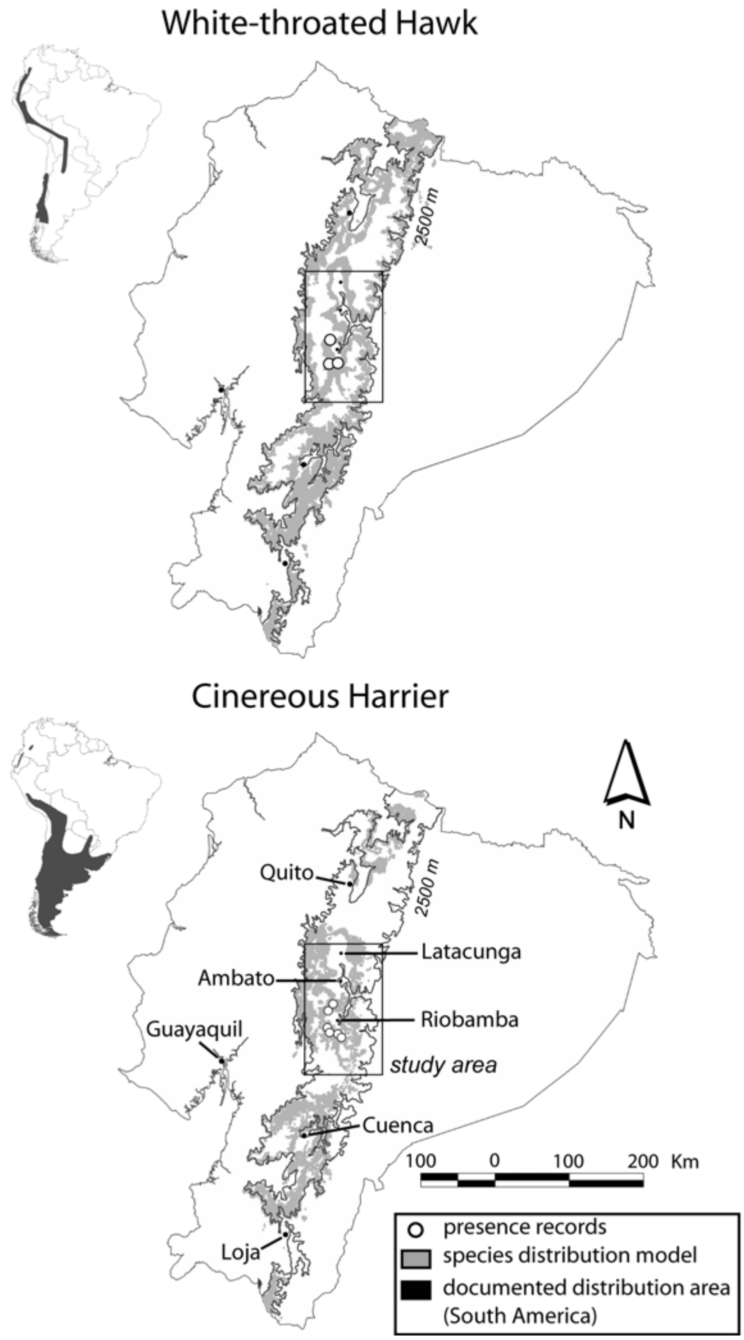

FIG. 1. Records and predicted distributions for the White-throated Hawk and Cinereous Harrier for the Ecuadorian Andes. Species distributions for South America were obtained from Ridgely *et al.* (2003).

among landscape variables. Moreover, the small number of presences in the dataset did not allow us to test for complex multivariate models. Probability of presence per pixel was transformed into presence or absence. The limit between the two, i.e. the threshold probability, was defined as the probability that maximized the percentage of successful prediction of known presence-absence records (Austin 2007). Linear effects highlighted the linear (positive or negative) relationship between a variable and a species. Quadratic effects demonstrated that species had an optimum for that variable, occurring for a narrow range of values. We restricted spatial extrapolation to the Andes above 2500 m.

Since our sampling design did not establish that all classes of land cover had been equally covered, we tested for biased coverage by a resampling procedure. A number of points equal to the point count number were randomly selected from the entire study area. We repeated this selection 1000 times to obtain a null distribution for variable ranges (upper and lower boundaries). If the actual variable ranges for sampled localities did not deviate significantly from the distributions obtained by random resampling, it was concluded that our dataset provided an unbiased coverage of actual environment in the study area (Raes & ter Steege 2007).

RESULTS

Relative abundance. We obtained 14 records for the White-throated Hawk and seven for the Cinereous Harrier from six locations each (Table 1, Fig. 1). The species were recorded on 9% and 7% of survey days respectively (N = 105).

Habitat, climatic and landscape correlates of occurrence. The resampling test demonstrated that the surveyed sites provide an unbiased coverage of the range of variation per landscape variable in the study area. Frequencies of land-cover types were not significantly different from expected from random sampling (all $P > 0.3$), hence our dataset and models provided an unbiased characterization of habitat use and distribution for both species in the study area.

Presence of the White-throated Hawk was mainly associated with elevation and mean temperature whereas mean precipitation and aridity index had a relatively small influence (Table 2). Significant quadratic effects suggest that the species has optimum ranges for all four variables. According to habitat correlates, presence was associated with the shrubby and herbaceous vegetation land cover category.

Presence of the Cinereous Harrier was mainly associated with mean precipitation with a dry optimum range (Table 2) followed by weaker effects of the aridity index (arid optimum range) and elevation (positive association). According to habitat correlates, presence of the Cinereous Harrier was positively associated with the shrubby and herbaceous vegetation land cover category. Distance to water did not influence the probability of presence (Table 2).

Predicted distribution ranges. Extrapolations of potential distribution ranges in the inter-Andean valleys of Ecuador (Fig. 1) were obtained with the final GAMs for each species (Table 2). Although the environmental correlates of presence were similar for both species (Table 2), the differences in variable contributions (cf. *Wi*) conduced to distinct distributions.

DISCUSSION

Both species were observed on less than 10% of field survey days. These low frequencies classified them as rare to very rare in the study area (lower than 25%, Ridgely & Greenfield 2001), as has been reported for the

TABLE 1. Records of White-throated Hawk (WTH) and Cinereous Harrier (CH) from Chimborazo Province, Ecuador, 2004; dates followed by field survey days (no.) within 1 km radius around points of occurrence. All birds were in flight unless another behavior is mentioned. [1]Habitat (based on field notes): Agric. = agricultural areas and dry grassy-shrubby pastures, Euc. trees = *Eucalyptus* stands, Lake = lake and reed bed, Páramo = grassy, humid páramo.

Species	Location, nearest village	Geographical coordinates	Elevation (± 50 m)	Dates of records (no. days)	Habitat[1]. Observation
WTH	Paquibuc San Pablo, San Andres	01°33'56"S, 73°43'45"W	3209	25 June (5)	Agric., Euc. trees. Two join and soar together (11:51 h); one sitting on a *Eucalyptus* tree (11:56 h); one in flight (14:09 h). No nest in the eucalyptus stand.
WTH	Los Angeles, Colta	01°47'33"S, 78°44'25"W	3270	11, 12, 19 June (8)	Agric., Euc. trees. Two adults soaring high (13:55 h, with one *Buteo polyosoma*); one possible immature (streaked underparts; 10:03 h); one soaring at low altitude (09:33 h); one adult (14:00 h, 17:54 h); one (13:30 h).
WTH	Chacabamba, Columbe	01°48'29"S, 78°44'28"W	3276	15 June (5)	Agric., Euc. trees. One (11:59 h) attacked by one *Falco sparverius*.
WTH	Santa Rosa, Flores	01°48'35"S, 78°38'48"W	3120	11, 12 May (4)	Agric., Euc. trees. One possible adult (14:00 h).
WTH	San Rafael, Columbe	01°48'58"S, 78°44'12"W	3238	16 June (5)	Agric., Euc. trees. One (13:22 h) attacked by one *F. sparverius*.
WTH	Quishuar Alto, Columbe	01°50'30"S, 78°44'20"W	3365	13 June (4)	Agric., Euc. trees. One adult (11:52 h); one (12:10 h).
CH	Sanancajas, Urbina	01°28'49"S, 78°41'55"W	3610	6 May (1)	Páramo. One male.
CH	Vicinity of San Andres	01°33'40"S, 78°44'58"W	3293	30 June (5)	Agric., Euc. trees. One male (13:56 h).
CH	Laguna de Colta	01°44'10"S, 78°45'40"W	3299	13 March, 15 June (7)	Lake, Agric. One (c. 16:00 h); one pair (13:41 h)
CH	Los Angeles, Colta	01°47'33"S, 78°44'25"W	3270	11 June (8)	Agric., Euc. trees. One second-year male hunting in a shrubby area dominated by *Lupinus* sp.
CH	Santa Rosa, Flores	01°48'35"S, 78°38'48"W	3120	12 May (4)	Agric., Euc. trees. One male.
CH	Cecel Grande, Flores	01°50'40"S, 78°36'36"W	3072	13 May (2)	Agric. One female, in shrubs dominated by *Lupinus* sp.

TABLE 2. Significant associations between species and eco-climatic variables (1-km^2 resolution) tested by χ^2-tests of GAM comparisons. Contribution of each variable to the distribution model is quantified by *Wi* (Akaike weights) followed in parenthesis by the sign of the slope for linear effects or Q for quadratic effects, and the range of values (95% confidence intervals) associated with species presence. Range of values for the study area and unit follow each variable's name. *** = $P < 0.0001$; ** = $P < 0.001$.

Description (range in study area, units)	White-throated Hawk	Cinereous Harrier
Land cover type (shrub and herbaceous, forest, cropland)	All individuals observed on shrub and herbaceous land-cover class	
Mean monthly temperature (3.3–17.8°C)	0.30 (Q, 7.6–14.2) ***	ns
Mean monthly precipitation (43–191 mm)	0.10 (Q, 54–118) **	0.87 (Q, 63–82) ***
Aridity index (0.22–1.36 mm/°C)	0.12 (Q, 0.31–0.80) **	0.10 (Q, 0.33–0.77) ***
Elevation (2500–4300 m)	0.48 (Q, 2680–3550) ***	0.03 (+, 2550–4055) **

rest of their distributional range (Jimenez & Jaksic 1988, Fjeldså & Krabbe 1990, Jaksic *et al.* 2001, Ridgely & Greenfield 2001, Figueroa Rojas *et al.* 2002, Restall *et al.* 2006, Schulenberg *et al.* 2007, Silva-Rodríguez *et al.* 2008).

The presence of the White-throated Hawk was mostly related to elevation. In the study area, the optimal altitudinal range was 2680–3550 m. This range is higher than the altitudinal ranges given for the region (2100–3000 m, Krabbe *et al.* 1998) and for Ecuador (2100–3250 m, Krabbe *et al.* 1998; 2200–3200 m, Ridgely & Greenfield 2001). Elsewhere in the Andes, the species occurs up to 3700 m (Schulenberg *et al.* 2007). All records were associated with the 'shrubby and herbaceous vegetation' land cover category, which covers 53% of the study area. This habitat does not correspond to the descriptions of the usual habitats for the species, i.e. humid and cloud montane forests and woodlands adjacent to open areas in the upper subtropical and temperate zones and dwarf forest patches (Fjeldså & Krabbe 1990, Krabbe *et al.* 1998, Ridgely & Greenfield 2001, Trejo *et al.* 2007, Silva-Rodríguez *et al.* 2008). The lack of association between our records and forest may have three reasons. First, during migration time, the species would depend less on forests, and more on shrubby and grassland habitats (Pavez 2000). If observed birds were migrants (cf. hereafter), then association with the forest cover may be weak. Second, subtropical and temperate humid montane forest - the primary habitat for the species in the northern Andes - is not represented in our study area. Hence, the occurrence of the species in this habitat cannot be analyzed with our data. Third, in the study area, the dominant form of forest was *Eucalyptus* tree plantations. Actually, all records of the White-throated Hawk were obtained from hilly, agricultural lands (potatoes, corn, wheat, barley, and quinoa cultivations) and grassy-shrubby pastures with scattered stands of *Eucalyptus* trees (Table 1). These *Eucalyptus* tree plantations represented c. 10–20% of the landscape at sites of occurrence in the study area, but they were never the dominant land cover at the pixel scale. Hence, even if the species is strongly dependent on *Eucalyptus* cover at the fine scale, this could not be detected with 1-km^2 pixels. The association of the species with *Eucalyptus* trees had already been mentioned as a peculiarity of Ecuador by Fjeldså & Krabbe (1990). In its breeding range, the species does not use *Eucalyptus* plantations (recorded only once, Silva-Rodríguez *et al.* 2008). Hence, in the inter-Andean valleys of Ecuador, the forest-dwelling White-throated Hawk would largely rely on *Eucalyptus* tree stands surrounded by open, cultivated lands for stop-over and/or wintering. Both during the breeding (Gelain *et al.* 2001, Figueroa Rojas *et al.* 2002) and the non-breeding period (no effect of the POP variable), the species occurs in human-modified habitats. This apparent tolerance to human disturbance indicates either that some human-modified habitats are actually suitable for the species, and/or that the disappearance of its native habitat may force it to exploit sub-optimal surrounding habitats.

According to the distributional range, these observations are the first records of the White-throated Hawk for central Ecuador. Only one unconfirmed record had been obtained from the northeast of Chimborazo Province (Ridgely & Greenfield 2001). In agreement with Krabbe *et al.* (1998), our results suggest that the species could occur all along the Ecuadorian Andes (Fig. 1). Formerly the species was known from the northern highlands of Ecuador only (provinces of Carchí to Pichincha; Ridgely & Greenfield 2001), including inter-Andean valleys, and from the eastern slope of the Andes (Fjeldså & Krabbe 1990; south of the Cañar Province, Ridgely & Greenfield 2001). Our results (Fig. 1) suggest that the species may occur on the western slope of the Andes in central and southern Ecuador. This finding is supported by only one record (Ridgely & Greenfield 2001) and predictions of occurrence (Krabbe *et al.* 1998) for Azuay Province. In agreement with Ridgely & Greenfield (2001), but *contra* Fjeldså & Krabbe (1990), our results also show that the species is not restricted to Andean ridges where most humid montane forests are located, and also occurs in more arid and open parts of the central inter-Andean valley. The actual distribution range is wider than illustrated in Fig. 1 including subtropical and temperate montane forests on Andean slopes and ridges (Krabbe *et al.* 1998). Unfortunately, these native forest habitats could not be included in our predictions since we did not survey them.

What is the status of the White-throated Hawk in central Ecuador? Two scenarios are possible: breeding residents (N. Krabbe pers. com. *in* Trejo *et al.* 2007) and/or migrants or wintering individuals of Austral origin. We did not obtain any evidence of breeding activity and the habitat did not correspond to the known breeding habitat of the species. If birds were local residents, they could have been wanderers from neighboring patches of favorable habitat, i.e. humid and dwarf montane forests, which were 17 ± 6 (SD, range 10–28) km from the sites where we recorded the species. Our records are more suggestive of an Austral migratory origin. The seasonal increase in the frequency of observation is congruent with the post-nuptial migration timing described for the species: the frequency increased from 0% of field days in March–April (N = 40 days) to 7% in May (N = 28 days), and to 28% in June (N = 25 days; Table 1). Birds depart from the breeding sites in March–April and return in September–October (Gelain *et al.* 2001, Silva-Rodríguez *et al.* 2008; reviewed in Trejo *et al.* 2007). Records of active migrants suggest that northward migration mainly takes place in March (90% of records for central Chile, Pavez 2000) and April (southern Chile and north-eastern Argentina, Pavez 2000, reviewed in Trejo *et al.* 2007). If the birds that we observed were of Austral origin, our records suggest an arrival of post-nuptial migrants around the equator in June. This observation is congruent with the first satellite-tracked, migrating White-throated Hawk overflying the southern Ecuadorian border between 26 and 29 May 2008 (L. Sympson *in litt.*). Based on dates of available records, Ridgely & Greenfield (2001) also suggested that most or all White-throated Hawks observed in Ecuador were Austral migrants or wintering birds.

Presence of the Cinereous Harrier was mainly influenced by mean precipitation. Its optimal precipitation and aridity ranges indicate that the species inhabits relatively dry parts of the study area (Table 2). The linear increase in the probability of presence with elevation suggests that the optimum elevation for the species was close to, or above, 3700 m, the highest altitude that we surveyed. This corresponds to the elevation range given for the northern Andes (3000–4000 m, Ridgely & Greenfield 2001; up to 4500 m in Peru, Fjeldså & Krabbe 1990). Habitats where the species occurred in the study area (Table 1, 2) corresponded well with the description for the rest of Ecuador (Ridgely & Greenfield 2001): open, shrubby grasslands and páramo (high-altitude grasslands, above 3200 m), and agricultural terrains. Our results also confirm that in Ecuador (Ridgely & Greenfield 2001), and contrary to populations from central and southern Andes (Jimenez & Jaksic 1988, Fjeldså & Krabbe 1990, Restall *et al.* 2006, Schulenberg *et al.* 2007), the Cinereous Harrier does not depend on wetlands (Table 1, 2). Our model predicted a continuous occurrence of the Cinereous Harrier along the Ecuadorian Andes (Fig. 1). The northern part of this predicted range is in agreement with the extrapolated distribution range for Ecuador (Ridgely & Greenfield 2001), a continuous occurrence in the Andes north of Chimborazo Province. Further south, between central Ecuador and central Peru (Huánuco Province; Fig. 1; Schulenberg *et al.* 2007), the species does not occur in the Andes. This absence may be related to the relatively low altitude of the mountains in northern Peru. Only one record confirms occurrence of the species in southern Ecuador: one 19-th century specimen from Cañar Province (Fjeldså & Krabbe 1990, Ridgely & Greenfield 2001). Although this gap may seem biologically inexplicable (Ridgely & Greenfield 2001), and despite our model suggesting that suitable conditions exist in southern Ecuador, occurrence of the species south of Chimborazo Province seems unlikely. The distributional gap for Pichincha Province, south and east of Quito, is largely unwarranted. The species has been observed both in the western (volcanos Pichincha and Corazón, D. Cisneros-Heredia *in litt.*) and the eastern cordilleras (area of Papallacta, Pichincha Province; Antisana Ecological Reserve, Napo Province; D. Cisneros-Heredia, R. Ahlman *in litt.*). However, the species may well be absent from the inter-Andean valley (Pichincha Province) since it has never been observed there.

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