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Research Paper

## Distribution, migratory behavior, and conservation of Hudson's Canastero *Asthenes hudsoni* (Furnariidae): a grassland specialist from the humid Pampas

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**ABSTRACT.** Hudson's Canastero, *Asthenes hudsoni* (Furnariidae) is a secretive passerine from the Río de la Plata grasslands of South America. It is considered near threatened, but little is known about its distribution and seasonal movements. We performed a thorough revision of historical and recent records of the species and estimated its original and current geographic distribution using niche modeling based on climatic and land cover information. We found that *A. hudsoni* is not widespread across the Río de la Plata grasslands but mostly restricted to the humid pampas in Argentina, with isolated populations in central Argentina and SE Brazil. Most records north of the humid pampas in Argentina and Uruguay correspond to wintering individuals, revealing that the species is a partial seasonal migrant. Our distribution models indicate that its original area of occupancy may have been reduced by 65% to a current ~50,000 km<sup>2</sup>, with a stronghold in the flooding Pampas in eastern Buenos Aires province. However, because of the specific microhabitat requirements of the species, we suspect that this figure underestimates the extent of appropriate habitat available, and that *A. hudsoni* could be very close to the threshold of area of occupancy for vulnerable species under IUCN criteria. Further research on habitat requirements, distribution, and population trends are urgently needed.

### Distribution, comportement migratoire et conservation du Synallaxe de Hudson *Asthenes hudsoni* (Furnariidae) : un spécialiste des prairies de la pampa humide

**RÉSUMÉ.** Le Synallaxe de Hudson, *Asthenes hudsoni* (Furnariidae) est un passereau discret des prairies du Río de la Plata en Amérique du Sud. Il est considéré comme quasi menacé, mais on sait peu de choses sur sa répartition et ses mouvements saisonniers. Nous avons effectué une révision complète des enregistrements historiques et récents de l'espèce et estimé sa distribution géographique originale et actuelle en utilisant un modèle de niche basé sur des informations climatiques et de couverture terrestre. Nous avons constaté que *A. hudsoni* n'est pas répandu dans les prairies du Río de la Plata, mais qu'il est surtout limité à la pampa humide en Argentine, avec des populations isolées dans le centre de l'Argentine et le sud-est du Brésil. La plupart des enregistrements au nord de la pampa humide en Argentine et en Uruguay correspondent à des individus hivernants, ce qui révèle que l'espèce est un migrateur saisonnier partiel. Nos modèles de distribution indiquent que sa zone d'occupation initiale pourrait avoir été réduite de 65% pour atteindre actuellement ~50 000 km<sup>2</sup>, avec un bastion dans les pampas inondées de l'est de la province de Buenos Aires. Cependant, en raison des exigences spécifiques de l'espèce en matière de microhabitat, nous soupçonnons que ce chiffre sous-estime l'étendue de l'habitat approprié disponible et que *A. hudsoni* pourrait être très proche du seuil de la zone d'occupation des espèces vulnérables selon les critères de l'IUCN. Il est urgent de poursuivre les recherches sur les exigences en matière d'habitat, la distribution et les tendances de la population.

**Key Words:** *Asthenes hudsoni*; conservation; distribution; Furnariidae; grasslands; migration; pampas; Río de la Plata

## INTRODUCTION

Hudson's Canastero, *Asthenes hudsoni*, is a scarce inhabitant of lowland grasslands in the Río de la Plata region in South America (Remsen 2003). It can be found in tall humid grasslands, usually near brackish marshes (Isacch and Martínez 2001, Isacch et al. 2004), particularly in grasslands composed of two strata: a high

stratum formed by clumps of tall grasses (tussocks) and a low stratum formed by runways of short grass or bare ground (Wetmore 1926, Isacch and Martínez 2001, Isacch and Cardoni 2011). In dimensions and plumage, *A. hudsoni* resembles an *Anthus pipit* (Sclater and Hudson 1888, Wetmore 1926), except for its contrasting throat patch, pointed rectrices, and wing bands characteristic of many spinetails. Its nest, which consists of a

dome made mostly with grass and embedded at the base of a tussock (Sclater and Hudson 1888, Wetmore 1926, Narosky et al. 1983), also indicates the specialization of *A. hudsoni* for grasslands.

*A. hudsoni* is regarded as near threatened globally mainly because of suspected declines in its populations due to habitat loss (BirdLife International 2021). It is already considered vulnerable in Argentina (Ministerio de Ambiente y Desarrollo Sustentable and Aves Argentinas 2017) and scarce in Buenos Aires province (Narosky and Di Giacomo 1993, Codesido et al. 2012), where its preferred habitat is being reduced by intensive farming practices (Agra et al. 2015, Codesido and Bilenca 2021a). In Brazil, the species is only known from a handful of sites in southern Rio Grande do Sul (Bencke 2001, Zimmer and Whittaker 2009), and a single record is known from Paraguay (Vaurie 1980, Hayes 1995). In Uruguay it has been reported since the 19th century (Palerm 1971) and it is considered uncommon and vulnerable, but information is scarce (Azpiroz 2001, Azpiroz et al. 2012).

Here we evaluate the geographic distribution and seasonality of *A. hudsoni*, revise historical records, provide new records for Uruguay, and generate distribution models to estimate the area of occupancy and occupancy changes due to habitat loss. Our findings provide a new view on the distribution, migratory behavior, and conservation status of *A. hudsoni*.

## METHODS

### Distributional data

To reevaluate the geographic distribution of *A. hudsoni* and its possible historical change we reviewed both historical and contemporary distributional records. We obtained distributional records from museum specimens, published accounts, and public databases. We searched the literature for records of *Asthenes hudsoni* or its older synonyms *Synallaxis hudsoni*, *Siptornis hudsoni*, and *Thripophaga hudsoni*. We consulted online museum databases including global repositories, such as Ornis (<https://sites.google.com/site/ornisnet>), VertNet (<http://www.vertnet.org/>), and Gbif (<https://www.gbif.org/>). We tracked the whereabouts of specimens and requested further information and photographs. We also queried the online citizen science database eBird (eBird Basic Dataset, 2020, <https://ebird.org/home>) focusing on records that had verifiable evidence, such as photos or sound recordings, and consulted the community of ornithologists and birdwatchers participating in the mailing list Ornithologiauy. Finally, we report our own records based on extensive fieldwork in Uruguay. If not georeferenced already, we georeferenced records to the global geographic coordinate system using the Ornithological Gazetteers (Paynter 1995) or standard georeferencing procedures (Wieczorek et al. 2012) in Google Earth 6.1 (Gorelick et al. 2017).

Reported specimens were housed at Museo Argentino de Ciencias Naturales, Buenos Aires (MACN, 42 specimens), American Museum of Natural History, New York (AMNH, 14), National Museum of Natural History, Smithsonian Institution, Washington (NMNH, 10), University of Michigan Museum of Zoology, Ann Arbor (UMMZ, 8), Natural History Museum, Tring (BMNH, 6), Museum of Comparative Zoology, Harvard University, Cambridge (MCZ, 4), Field Museum of Natural

History, Chicago (FMNH, 3), Museo Nacional de Historia Natural, Montevideo (MNHN, 2), Michigan State University Museum (MSU, 1), and Western Foundation of Vertebrate Zoology (WFVZ, 1). Details of specimens and literature records are provided in Appendix 1.

### Geographic distribution modeling

Using the revised distributional records, we estimated the past, present, and seasonal geographic distributions of *A. hudsoni*. To investigate distributional shifts associated with seasonality we classified occurrences into breeding and non-breeding seasons. We divided the year into two seasons with limits at the vernal and autumnal equinoxes: we considered breeding season records those obtained in spring and summer (22 September to 20 March), and non-breeding season records those obtained in autumn and winter (21 March to 21 September). This framework has been used before for birds of the humid pampas (Isacch and Martínez 2001) and is compatible with the information on breeding activity in *A. hudsoni* (Narosky et al. 1983, Fraga and Narosky 1985, Salvador 2013, Trofino Falasco et al. 2022). We then evaluated potential differences in the distribution of records (latitude and longitude) between breeding and non-breeding seasons using a non-parametric Mann-Whitney *U* test.

We generated distribution models based on climatic and topographic information to produce a primary estimate of the species geographic distribution. In case of significant seasonal shifts, we modeled breeding and non-breeding distributions separately, with localities where the species was reported as year-round resident included in both models. In a second step, we used high-resolution land cover data to filter out natural unsuitable habitats (mainly water bodies and forests) and obtain an estimate of the past distribution of the species before large-scale human impacts. In a third step we subtracted agricultural plots and urban environments to assess habitat loss due to anthropogenic activities.

To generate the primary maps, we used the Maxent machine learning algorithm (Phillips et al. 2017). Maxent fits distribution models by contrasting the range of environmental conditions in the presence points with background points, a set of points that provide information about the background environmental conditions in the region (Phillips et al. 2006). As predictors, we used 19 bioclimatic variables plus annual average solar radiation and annual average water vapor pressure from WorldClim version 2 (Fick and Hijmans 2017). In addition, a layer of topographic slope was obtained from EarthEnv database (Amatulli et al. 2018) at a resolution of 30 arc-seconds (approximately 1 km).

Because distributional records were not the result of systematic or random sampling, they may be biased toward sites that are easily accessible or regularly visited by observers, and this may affect model accuracy. To correct for this bias, we used the “target group background” method (sensu Phillips et al. 2009), which consists of selecting background data from points where similar organisms have been observed because they are likely to present a similar bias. Therefore, we used records of all bird species in the region from eBird (eBird Basic Dataset 2020) to generate a sample of background points. Background points were sampled from a region defined by adding a 500 km buffer radius around the occurrence sites. Presence and background data sets often exhibit

some degree of spatial autocorrelation because of the proximity or clustering of sites, violating Maxent's assumption of spatial independence. To reduce spatial autocorrelation, we applied a spatial filter with a minimum allowed proximity between points of 2 km for both data sets (Kramer-Schadt et al. 2013). For a map of the occurrence sites, background sites, background region, and other details of the models see Appendix 2.

To avoid overfitting, we performed data-driven variable selection using the “varSel” function in the library *SDMtune* (Vignali et al. 2020) in R (R Development Core Team 2021). The varSel function evaluates highly correlated predictors (Spearman correlation higher than 0.6) and removes those whose removal produces the largest improvement in the model as assessed by the Akaike information criterion (AICc). The process is repeated until the remaining predictors no longer show high correlations. To tune hyperparameters of the models, we used the “optimizeModel” function of the R package *SDMtune* (Vignali et al. 2020), configured to find the regularization multiplier and the feature classes combination that together produce the model with the lowest AICc. Other Maxent parameters were kept at their default values.

We built the final past distribution maps by dividing the raw Maxent probability output by the percentage of natural land cover not suitable for the species in the cell, corresponding to the sum of land cover fraction of permanent water, seasonal water, trees, bushes, bare soil, and ice. Finally, we built current distribution maps by arithmetic division of the past distribution maps of each season by a layer of anthropic land cover not suitable for the species in the cell, corresponding to the sum of land cover fraction of cropland and urban areas. The land cover layers were obtained from the Copernicus Global Land Service: Land Cover 100 m: Collection 3: Epoch 2015 (Buchhorn et al. 2020), aligned before performing arithmetic operations with the Maxent output layer of 30 arc seconds resolution using bilinear resampling. The binary occurrence areas were determined from the continuous current and past distribution maps produced in the previous step, using a suitability threshold corresponding to a 25% omission rate (OR) of the presence data locations in the Maxent raw outputs.

## RESULTS

We first provide critical accounts of historical and recent records of *A. hudsoni* in regions outside the Argentine pampas and then present the results of the geographic distribution models.

### Uruguay

There are few records of *A. hudsoni* in Uruguay. The first is attributed to Dalglish (1881a, Cory and Hellmayr 1925, Palerm 1971), who received two collections of birds and eggs from Estancia Tala (32°48' S, 56°07' W; Fig. 1:1 [see numbers within Fig. 1 for numbered localities]), Durazno department, formerly part of Estancia San Jorge (Christison 1880). When describing the first collection, Dalglish (1881a) listed *Synallaxis hudsoni* Sclater, with a brief description of nest and habits. Upon further examination, the specimen was reidentified as *Anumbius annumbi* (Dalglish 1881b, probably specimen BMNH 1889.5.20.276), which agrees with the vernacular name (“espinero”) and the description of the nest (a large nest made of sticks on a tree) given by Dalglish (1881a). Dalglish (1884) did not list *A. annumbi* nor *S. hudsoni* when describing the second collection of birds and

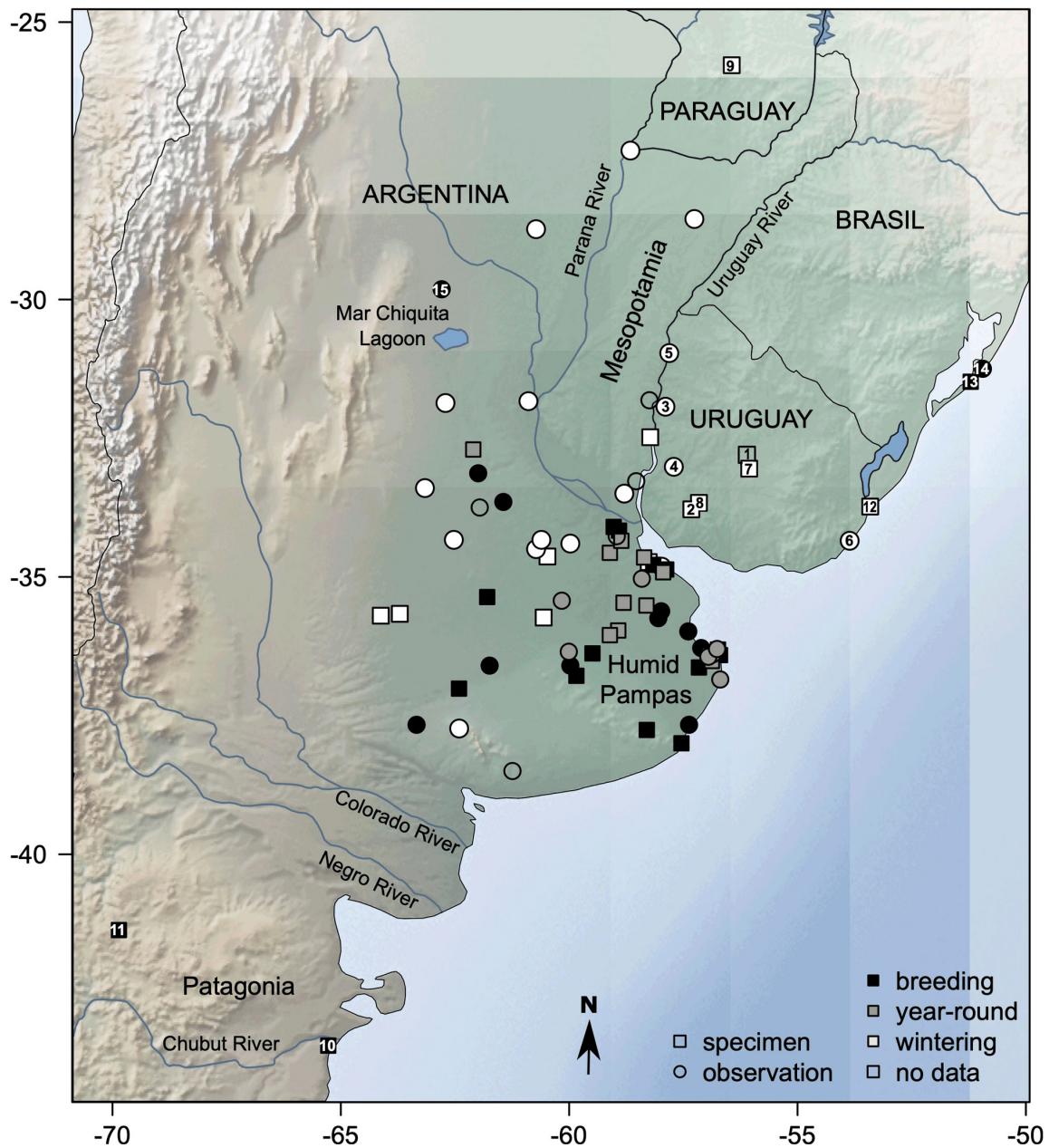
eggs. Nevertheless, there is a specimen of *Asthenes hudsoni* from Uruguay among the specimens that P. L. Sclater received from Dalglish (BMNH 1889.5.20.264). Dalglish probably believed that the new specimen was also *Anumbius* and for that reason did not mention it in the 1884 article. The specimen, an adult bird by plumage, was properly identified by P. L. Sclater as *A. hudsoni* in 1889, according to the BMNH catalogue (corroborated by us from photographs of the specimen). Specimens of *A. hudsoni* can appear superficially like those of *A. annumbi*, especially those that lack the dark throat patch, but identification is straightforward based on the absence of a rufous forehead and black spotting on malars. This specimen reported by Sclater (1890) is the first valid record of *A. hudsoni* for Uruguay.

A second specimen, an adult female (BMNH 1897.12.2.7, photograph examined), was collected by O. V. Aplin on 3 May 1893 at Estancia Santa Ana (33°40' S, 57°10' W, Fig. 1:2), near Arroyo Grande River, SW Flores department. Aplin declared to have seen the species on several occasions but provided no other specific records (Aplin and Sclater 1894).

There were no records of *A. hudsoni* from Uruguay during the entire first half of the 20th, nor during a period of active fieldwork and collecting in the 1950s and 1960s (Cuello and Gerzenstein 1962, Palerm 1971). The next records are those of Alfred Gepp, who found the species only twice during his field trips throughout Uruguayan territory. He found one individual on 29 August 1968 at Estancia Greenfields (Griffin family, not located) near Quebracho (31°56' S, 57°54' W; Fig. 1:3), Paysandú department, and three individuals on 30 July 1974 at Estancia Bichadero, Rio Negro department, between the main house and the Negro River (~3°01' S, 57°43' W; Fig. 1:4; A. Gepp's field notebook, this record was reported as occurring in August in Gore and Gepp 1978). Gore and Gepp (1978) also mentioned specimens collected in Colonia department by Dr. B. Rebuffo. We found two mounted specimens of *A. hudsoni* at the Museo Municipal de Colonia, which houses Rebuffo's collections, but the specimens lack any label or catalogue information. More recently, on 6 June 1988, Arballo (1990) reported one individual observed at El Espinillar (30°58' S, 57°49' W; Fig. 1:5), Salto department, and Gambarotta et al. (1999) found the species at Refugio de Fauna Laguna de Castillos (34°21'40" S, 53°52'10" W; Fig. 1:6), Rocha department, with records between May and September in the floodplain and tall grasslands.

During fieldwork in Uruguay, we obtained two additional records of *A. hudsoni*. On 1 April 1994, S. C. collected a specimen at Estancia San José (33°03'15" S, 56°04'25" W; Fig. 1:7), 22 km NNW El Carmen, Durazno department. The bird was found at 9:45 h in a natural grassland growing on a basaltic plateau on top of the Cuchilla Grande de Durazno divide. The plateau was grazed by cattle (*Bos taurus*) and sheep (*Ovis aries*), and showed a dense turf of short grass (< 5 cm) and tussocks of spear grass (*Stipa* sp.). The plateau was waterlogged because of a combination of recent heavy rains and impermeable soils. The bird (MNHN 5013), found on the ground among a patch of tussocks, was a juvenile, as evidenced by the spotted upper breast (Grant 1911, Cory and Hellmayr 1925) and an incompletely pneumatized skull. S. C. visited Estancia San José regularly, especially during summer, but no other record of *A. hudsoni* was obtained. On 3 September 2002, C. M. collected a specimen at

**Fig. 1.** Specimen and literature records of Hudson’s Canastero *Asthenes hudsoni* (Appendix 1). Numbered localities are mentioned in the text.



Estancia Santa Emilia (33°47' S, 57°20' W; Fig. 1:8), ~9 km north of Cardona, Soriano department. The bird, prepared as a skeleton/flat skin (MNHN 6140, USNM 657741: tissue only), was a young female (skull 10% pneum. Bursa 6 x 3 mm) in adult plumage. The bird was collected in a narrow strip of tall grass leading to a freshwater stock pond surrounded by shorter, grazed fields.

### Paraguay

Vaurie (1980) mentioned “southeastern Paraguay” as part of the geographic range of *A. hudsoni* but Ridgely and Tudor (1994)

considered that information unverified, and Hayes (1995) listed the species as hypothetical in Paraguay. However, Vaurie’s (1980) report is probably based on a specimen deposited in the British Natural History Museum: an adult female (BMNH 1908.12.14.149) from Villa Rica (Fig. 1:9), collected on 13 June 1906. No other record is known from the country (Hayes 1995, del Castillo and Clay 2005).

### Patagonia

Durnford (1877) found *A. hudsoni* in the lower Chubut River valley (Fig. 1:10). He considered the species “not uncommon”

and collected a male on 5 November 1875, now at Tring (BMNH 85.11.20.284, photographs examined). He also reported two sightings along the Senguier River, in SW Chubut province (Durnford 1878), but given the proximity of these records to the distribution of the similarly looking *A. anthoides*, we consider them unreliable. Another documented record from Patagonia is a male collected on 24 November 1920 in the middle of the Patagonian steppes, at Estancia Huanu-luan, SW Río Negro province (Peters 1923, MCZ 85470, photographs examined; Fig. 1:11). The spotted breast indicates that the specimen was a young bird. Other surveys in northern Patagonia did not find *A. hudsoni* (e.g., Wetmore 1926, Vuilleumier 1993).

Other specimen from Patagonia in institutional and online databases were misidentified. Specimens from General Roca, Río Negro province (USNM 227573, 227627) are *Asthenes pyrrholeuca*, not *A. hudsoni*, easily distinguished by its plain plumage, smaller size, and longer tail with rufous outer rectrices. A specimen from Cholíla (MACN 42937), in NW Chubut province, is *A. anthoides*, not *A. hudsoni*, distinguished by its darker and grayer plumage, and its shorter beak and tail (compared side by side at the MACN). Other specimens from localities outside the pampas that were erroneously identified as *A. hudsoni* are specimens of *A. pyrrholeuca* from Bahía Blanca (USNM 227572), Buenos Aires province, and Riacho Pilaga (USNM 227322), Formosa province. The absence of records of *A. hudsoni* in the lower Colorado and Negro rivers is also remarkable given the presence of extensive brackish marshes (Isacch et al. 2006a).

## Brazil

In Southern Brazil, *A. hudsoni* is known from a handful of localities and its breeding status is not confirmed (Bencke 2001, Zimmer and Whittaker 2009). Two birds were collected in July 1964 at Arroyo Chuí (Fig. 1:12), an additional specimen was obtained in December 1996 near Capão Comprido (Bencke 2001, Fig. 1:13), and more birds were recorded at the end of February 2006 near Lagoa do Peixe (Zimmer and Whittaker 2009; Fig. 1:14). These three localities lie in coastal plains, in a region of extensive wetlands. Records from August to February suggest a breeding population, but breeding activity, other than singing, has not been documented (Zimmer and Whittaker 2009, eBird 2020).

## Distribution models

We obtained records of *A. hudsoni* for 164 localities, 86 of which were museum specimens or literature records and 78 were eBird records with photos. After spatial filtering, we retained 131 sites, 71 from the breeding season and 60 from the non-breeding season. Non-breeding season sites showed a significant northerly shift of about two degrees (median latitude = -34.53) compared to breeding sites (median latitude = -36.30, Mann-Whitney test:  $W = 1372, p = 0.0005$ ) but a difference in longitude was not detected (median longitude: -58.73 vs. -58.06, Mann-Whitney test:  $W = 2382, P = 0.26$ ).

The estimated historical distribution during the breeding season shows suitable areas throughout most of the humid pampas, mainly in Buenos Aires province, Argentina, and with the most suitable area around Bahía de Samborombón in the extreme east of the province (Fig. 2). A second area of high breeding suitability

was identified in coastal plains of Río Grande do Sul, Brazil, around the mouth of Lagoa dos Patos. Uruguay and other areas in central Argentina are of low suitability. During the non-breeding season, the suitability is spread more inland and northward (Fig. 2). Using the centroids of the estimated distributions, the wintering displacement was estimated to be 150.8 km towards the NW.

The estimated current distribution, considering areas made unsuitable by incompatible human land use such as agriculture and urbanization, was considerably reduced (Fig. 3). Overall, using a threshold of 25% omission rate of the presence records, from an estimated historical area of 137,908 km<sup>2</sup>, the suitable breeding area has been reduced to 48,835 km<sup>2</sup>, which amounts to a reduction of 65%.

## DISCUSSION

Our review of records of *Asthenes hudsoni* and distribution modeling revealed significant aspects of the distribution, seasonality, and conservation status of the species. First, the species is rare outside the Argentine humid pampas, both historically and currently. Second, records to the north of the humid pampas, except for those in Brazil, occurred between April and September, suggesting that the species is present there as a winter visitor only, and that it may be at least partially migratory. Finally, the species has experienced an important reduction in suitable habitat due to human impacts.

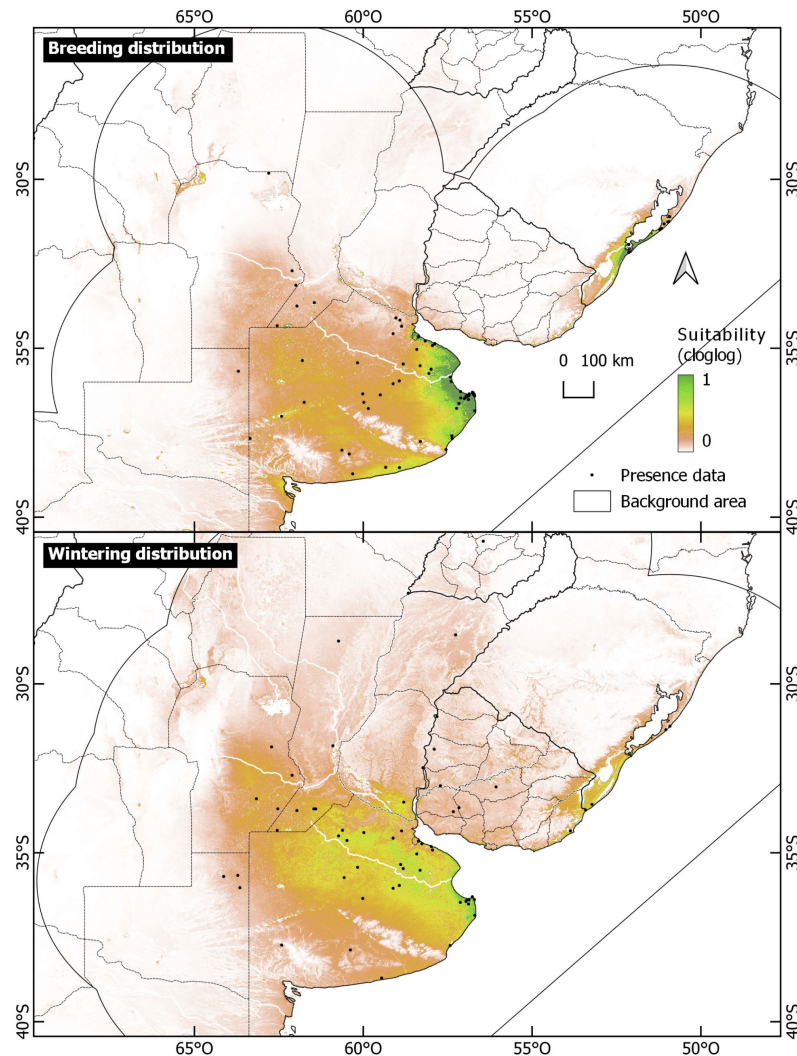
## Geographic distribution

Our revision of records of *A. hudsoni* indicates the bulk of its breeding distribution is restricted to the humid pampas. Furthermore, the distribution models suggest that the species is mostly restricted to the flooding pampas, a region of mostly natural grasslands on floodable soils in the eastern and central parts of the humid pampas (Soriano et al. 1991). In this region, the species occupies areas with tussocks of *Juncus acutus*, *Spartina densiflora*, or *Paspalum quadrifarium* near brackish marshes or lagoons (Isacch and Martínez 2001, Isacch et al. 2004, Lowen and Mazar Barnett 2010, Isacch and Cardoni 2011).

Records outside the humid pampas during the breeding season are rare. Records in Río Grande do Sul strongly suggest the existence of another breeding population. If this is the case, this population is likely small and highly vulnerable to natural and human disturbances (Zimmer and Whittaker 2009). In addition, the absence of neighboring breeding populations in Uruguay revealed by our analyses suggests that the Brazilian population is the only one to the north of La Plata River and may be isolated.

Historical records in northern Patagonia suggest that a local population was extirpated there. A population likely occupied marshes in the lower Chubut River floodplain in the 19th century (Durnford 1877). Since then, the lower Chubut River valley has been transformed into agricultural land, and no records of *A. hudsoni* have been reported in the area for more than a century, suggesting that the population has been extirpated. The juvenile collected in Patagonian steppes, in SW Río Negro province (Peters 1923), may represent a case of juvenile dispersal or migratory movement from an unknown Patagonian population or even from the pampas. Other specimen records of *A. hudsoni* in Patagonia turned out to be misidentifications. In addition to superficial

**Fig. 2.** Predictive maps of habitat suitability in the breeding and wintering seasons for Hudson's Canastero *Asthenes hudsoni*. Predictions correspond to the Cloglog outputs of Maxent distribution models based on bioclimatic variables and topography with the addition of a mask for unsuitable natural habitats such as water bodies and forests.

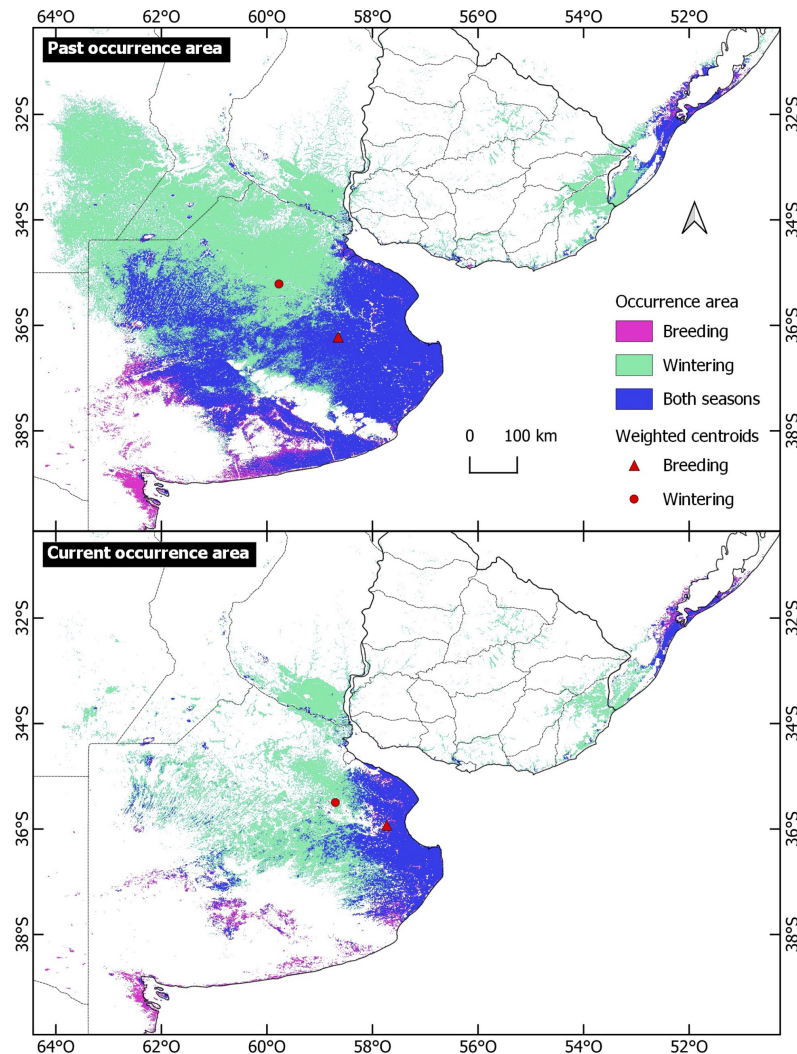


plumage similarities with other species, plumage polymorphisms (evident in throat patch presence and color in museum species), as well as varied and understudied vocal repertoire (López-Lanús and Roda 2012), may have compromised identifications. Exhaustive surveys should be conducted in appropriate habitat to determine whether a population of *A. hudsoni* still exists in northern Patagonia or along the floodplains of the lower Colorado and Negro rivers, which contain extensive *Spartina*-dominated brackish marshes (Isacch et al. 2006a). In the meantime, the region should be excluded from the current distribution of the species.

Given its secretive habits and cryptic plumage, it is possible that some breeding populations are overlooked. For example, two birds were seen in the Río Dulce wetlands (Fig. 1:15), in N Córdoba, on 27 November 1987 (Miatello et al. 2003). These

extensive brackish marshes associated with the Mar Chiquita lagoon may harbor a breeding population of *A. hudsoni* but confirmatory data are needed. The closest breeding record was obtained ~300 km to the south, around Villa María (Salvador 2013). Suitable habitats should be surveyed during spring and summer in search for breeding populations outside the humid Pampas. A major difference between the flooding Pampas and neighboring regions is their low and flat topography with poor drainage, which generate gradual ecotonal transitions between marshes and grasslands that the species seems to prefer (Isacch and Martínez 2001, Isacch et al. 2004). In Uruguay, coastal plains and brackish marshes are sparse and much more restricted in area, and the transition between marsh and upland grasslands is usually abrupt and demarcated by cut banks (Chebataroff 1960, Isacch et al. 2006a).

**Fig. 3.** Past and current occurrence area estimates for Hudson's Canastero *Asthenes hudsoni* based on the threshold 25% omission rate of the presence data locations from Maxent distribution models.



Our review of museum specimens and eBird images revealed instances of misidentification of *A. hudsoni*, usually involving other *Asthenes* species, *Anumbius annumbi*, but also *Anthus* pipits in the case of eBird records. We were able to reevaluate the identification of most extralimital specimens by direct examination of specimens or photographs, but additional misidentified specimens may still remain in collections and online databases. Proper documentation of distributional records is still important for understanding the distribution and status of poorly known and cryptic species, such as *A. hudsoni*.

### Migratory behavior

Our analyses confirmed that *A. hudsoni* is at least partially migratory. Argentine populations in the humid Pampas are present throughout the year but show seasonal fluctuations and were presumed to be partially migratory (de la Peña 1999, Isacch and Martínez 2001, Isacch et al. 2004). All records in Uruguayan

and Mesopotamian campos, other areas of northern Argentina, and Paraguay (Vaurie 1980, de la Peña 1999, Giraudo and Di Giacomo 2005, Pautasso et al. 2005) seem to represent wintering individuals (Fig. 1). Many of these records are far from brackish marshes or extensive tall grasslands. However, our observations in Uruguay suggest that the species may still seek grasslands with two strata (tussocks and short grass) during the non-breeding season.

The possibility that *A. hudsoni* is at least partially migratory is consistent with its wing morphology. Most *Asthenes* species do not fly much and have wings with low aspect ratio, as indicated by hand-wing indices around 10 (Claramunt et al. 2012). In contrast, the hand-wing index of *A. hudsoni* (19.6) indicates a higher aspect ratio that is more aerodynamically efficient for long-distance flights (Claramunt et al. 2012). The other two *Asthenes* species that have hand-wing indices above 17 are both partially migratory: *A. pyrrholeuca* (Remsen 2003) and *A. anthoides*

(Pantoja and Gallardo 2019). Because *A. anthoides* is the sister species to *A. hudsoni* (Derryberry et al. 2010) it is possible that high aspect ratio wings and the capacity for partial migration are ancestral to this pair of species. This wing morphology indicative of a higher degree mobility may also explain records far from breeding areas, including not only migratory movements but also juvenile dispersal movements (Claramunt 2021).

Our analysis of the annual cycle of *A. hudsoni* represents a first approximation. We divided the year into two seasons with boundaries set at the vernal and autumnal equinoxes as opposed to strict cut-off dates for the breeding period of the species, which may be more restricted to the spring (Narosky et al. 1983, Fraga and Narosky 1985, Salvador 2013). As more data on reproduction and movements accumulate, it will be possible to estimate the actual periods of breeding, movement, and wintering for *A. hudsoni*.

### Conservation implications

Our results suggest that the breeding distribution of *A. hudsoni* is more restricted than current distributional maps indicate (e.g., Remsen 2020, BirdLife International 2021). Our revision of records and distribution modeling suggest a new breeding range for the species that is mostly restricted to the flooding Pampas (Fig. 3). The species is extremely scarce away from the humid Pampas, with most records likely representing wintering or vagrant individuals.

The morphology, habitat, and nesting habits of *A. hudsoni* indicate that it is a highly specialized grassland bird (Sclater and Hudson 1888, Wetmore 1926, Narosky et al. 1983, Isacch and Martínez 2001, Isacch et al. 2004, Isacch and Cardoni 2011). Alternative classifications as a “facultative” grassland species (Vickery et al. 1999, Azpiroz et al. 2012) might be due to the association of *A. hudsoni* with marshes, potentially making it a wetland species instead. But the species is not a true wetland furnariid like *Phleocryptes melanops*, *Limnornis curvirostris*, *Limnornis sulphuriferus*, or *Spartonoica maluroides* that can forage and breed on emergent vegetation (Remsen 2003). *A. hudsoni* forages and nests on the ground and is absent in inundated areas. In fact, earlier references indicate that the species was widely distributed over open grassy country with no reference to closeness to marshes or water bodies (Sclater and Hudson 1888, Grant 1911). We speculate that a strong association of *A. hudsoni* with marshes might have emerged later, when intensification of grazing by livestock restricted the extent of tall grass to marshy areas and other marginal habitats.

At the regional scale, *A. hudsoni* is associated with the most conserved portions of the humid pampas, which correspond to the flooding pampas (Fig. 2; Codesido et al. 2013). The flooding pampas have been historically less affected by agriculture because of their water-saturated and saline soils (Baldi and Paruelo 2008). They contain numerous Important Bird Areas, and sustain the last remaining regional populations of the Pampas deer (*Ozotoceros bezoarticus*) and the Black-and-white Monjita (*Heteroxolmis dominicana*; Di Giacomo 2005).

Traditional cattle ranching—free-roaming livestock grazing on natural pastures—seems compatible with the persistence of *A. hudsoni* to some extent (Azpiroz et al. 2012, Codesido et al. 2013). In particular, in floodplains that tend to develop tall and dense

grasslands, cattle grazing can be beneficial by creating the short grass stratum required by the species for foraging (Isacch and Cardoni 2011). However, intense grazing, burnings, and herbicide applications can eliminate the tall grass that the species needs for cover and nesting (Rodríguez and Jacobo 2010, Agra et al. 2015, Codesido and Bilenca 2021a). The effect of alternative pasturing strategies—continuous versus rotational grazing—on *A. hudsoni* populations is still unclear (Isacch and Cardoni 2011, Vaccaro et al. 2020, Codesido and Bilenca 2021b).

Temporal trends in abundance have not been quantified for *A. hudsoni*. The species was considered common and widespread in the 19th century and early 20th century (Sclater and Hudson 1888, Grant 1911). However, during the 20th century, urban areas, agriculture, and pine plantations expanded across coastal and inland lowlands in Argentina, Uruguay, and Brazil at the expense of marshes and grasslands (Bencke et al. 2006, Bilenca and Miñarro 2004, Azpiroz et al. 2012, Booman et al. 2012, Rodríguez-Gallego et al. 2012). From 2000 to 2014 alone, nearly 23% of natural grasslands were converted to agriculture (Baeza and Paruelo 2020). Today, *A. hudsoni* is scarce even in the areas predicted as highly suitable in the humid pampas (Narosky and Di Giacomo 1993, Codesido et al. 2012, Ministerio de Ambiente y Desarrollo Sustentable and Aves Argentinas 2017). Recent surveys in coastal marshes near Buenos Aires have not detected the species (Isacch et al. 2006b). Moreover, even in its current stronghold in the flooding pampas, new technologies, such as application of herbicides and plantation of the salt-tolerant *Lotus tenuis* for forage, are deteriorating natural grasslands and increasing grazing pressure at an alarming pace (Rodríguez and Jacobo 2010, Agra et al. 2015, di Bella et al. 2015, Codesido and Bilenca 2021b). Therefore, although difficult to quantify, *A. hudsoni* likely experienced long-term and ongoing habitat loss and potentially an associated population decline.

Our estimates of potential distribution and current suitable habitat suggest that the species may have experienced a reduction of 65% of its original area of occupancy. This reduction probably occurred mostly during the late 20th century and early 21st century with the expansion of agriculture over the humid pampas (Baldi and Paruelo 2008, Baeza and Paruelo 2020). Our estimates are well above the area of occupancy threshold for IUCN criteria for vulnerable species (IUCN 2019). However, we suspect that the actual area of occupancy of *A. hudsoni* is smaller than what our models predicted. In particular, most of the suitable area identified in the flooding pampas of eastern Buenos Aires province is occupied by cattle ranches that are dominated by short-grass prairies, where suitable habitat for *A. hudsoni* would be restricted to borders of marshes or water bodies that preserve tall grass tussocks. Therefore, we suspect that the actual area of occupancy of *A. hudsoni* may be at least an order of magnitude smaller than what our estimates suggest. If this is the case, *A. hudsoni* would be very close to the threshold of area of occupancy for vulnerable species under criteria A4c (IUCN 2019). In Argentina, where the large majority of *A. hudsoni*'s global populations resides, the species is already considered Vulnerable (Narosky and Di Giacomo 1993, Ministerio de Ambiente y Desarrollo Sustentable and Aves Argentinas 2017). Further studies of distribution, habitat requirements, and population trends are urgently needed to define the global conservation status of *A. hudsoni* and propose effective strategies for its conservation.



Responses to this article can be read online at:  
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**Appendix 1.** Distribution models details

*Please click [here](#) to download file 'appendix1.xls'.*

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## Appendix 2: Distribution Models Details

### Breeding Season Model

Permutation importance of the variables selected using the variable selection algorithm:

Variable	Permutation importance	sd
bio03	26.7	0.021
vapr_mean	24.7	0.014
topo_slope	22.2	0.018
srad_mean	20.1	0.011
bio17	5.3	0.008
bio13	1	0.002

Statistic of the fitted model

Regularization multiplier: 0.75

Feature class combination: quadratic, hinge

Train locations: 16082 (presence 71; background locations 16011)

AUC: 0.91

### Non-breeding Season Model

Permutation importance of the variables selected using the variable selection algorithm:

Variable	Permutation importance	sd
topo_slope	48	0.032
vapr_mean	30.1	0.031

bio02	14.9	0.022
srad_mean	7	0.007

Statistic of the fitted model

Regularization multiplier: 1

Feature class combination: product, hinge

Train locations: 16053 (presence 60; background locations 15993)

AUC: 0.85

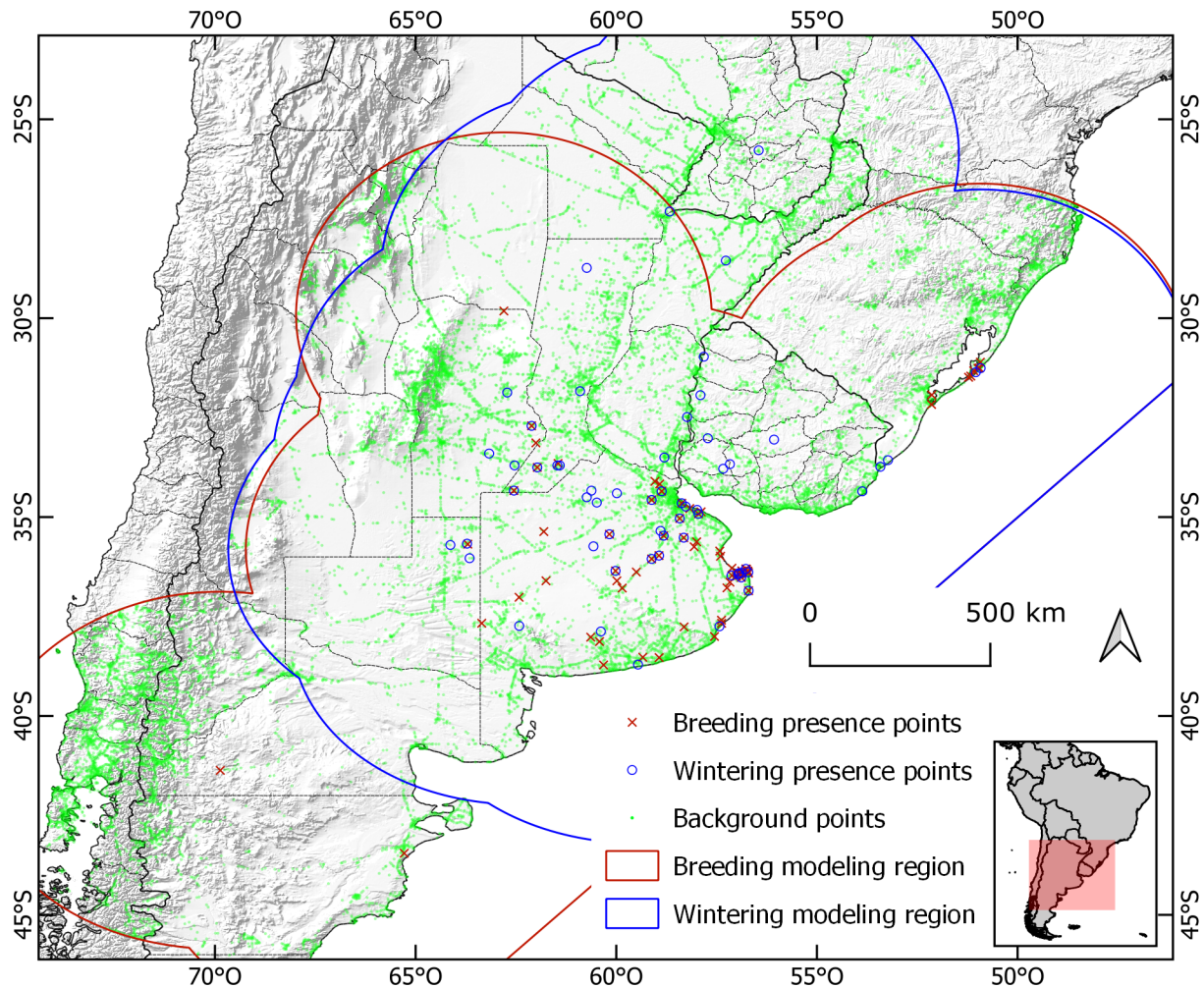


Figure A.2.1. Presence locations for *A. hudsoni* used to training species distribution models. Red and blue polygons represent the extent of the modeling region (only on land) for the breeding and wintering seasons, respectively. Background point in green correspond to eBird localities for all bird species.