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Claudina Solaro & José Hernán Sarasola

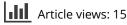
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Natal dispersal and philopatry of Chimango Caracaras (*Milvago chimango*) in suburban, rural and natural habitats, determined by band recovery and re-sighting data

Claudina Solaro and José Hernán Sarasola

Centro para el Estudio y Conservación de las Aves Rapaces en Argentina (CECARA), Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa (UNLPam) & Instituto de las Ciencias de la Tierra y Ambientales de La Pampa (INCITAP), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Santa Rosa, La Pampa, Argentina

ABSTRACT

Natal dispersal is a process whereby birds move from their birthplace to the site of their first attempt at reproduction. This process has strong implications for the dynamics and genetic structure of populations. However, studies on the dispersal of neotropical birds of prey are scarce. Here we investigated the post-fledgling and natal dispersal and philopatry of a common but poorly studied raptor, the Chimango Caracara (Milvago chimango) through band recovery and resighting data analysis across human modified and natural environments. During 10 years of study we banded 1738 individuals, with 793 banded as nestlings or fledglings in suburban, rural and natural habitats of central Argentina. We determined the dispersal distance for 94 individuals, 80 of which were recaptured at their natal site. Nine individuals moved between 5 and 120 km during the post-fledgling period (i.e. prior to their first breeding attempt) and five had natal dispersal distances (i.e. from natal to definitive breeding sites as adults) that varied between 10 and 800 km. Throughout band re-sighting we determined that Chimango Caracaras were able to breed at an age of 2 years old. Individuals tended to disperse to similar colonies and habitats as their natal sites (i.e. similar type of colony and degree of anthropogenic disturbance). Although most Chimango Caracaras exhibited short-distance dispersal (<10 km), some individuals may disperse over large distances (≈ 800 km). Our study shows for the first time the impact of natal area on breeding grounds in Chimango Caracara with consequent predictions for population structuring of this species.

Introduction

Natal dispersal refers to the movement of individuals from their natal site to the site of their first breeding attempt (Greenwood 1980; Ronce 2007). This process may have strong consequences for both individuals and populations by affecting genetic structure and gene flow within and between populations (Clobert et al. 2012). Moreover, dispersal may affect lifetime fitness by allowing individuals to acquire mates and breeding sites and to colonise new areas (Bowler and Benton 2005; Serrano and Tella 2012). In addition, individuals that disperse (or not) but then return and are faithful to their natal area to breed show natal philopatry (Gratto et al. 1985). In long-lived species such as birds of prey, natal dispersal movements are difficult to study because of the distances and time involved in this process, resulting in little information on the complexities of the dispersal process (Clobert et al. 2001; Penteriani and Delgado 2009). For these same reasons, compared to short-lived birds, even less is known about the post-fledgling movements of raptors during the period prior to their first reproductive attempt

(Morrison and Wood 2009). The natal dispersal process of raptors can be affected by diverse individual, social and spatial factors. In the first case, the sex and experience of dispersing birds can be important factors because the sex that invests more in reproduction is predicted to disperse shorter distances, and because more experienced birds are predicted to have higher site fidelity (Serrano *et al.* 2001; Forero *et al.* 2002). Second, individuals rely on cues from conspecifics to decide where to settle, with a greater number of dispersers recruited in larger colonies (Serrano *et al.* 2003, 2004). Lastly, distance among subpopulations can influence dispersal rate, since travelling to distant subpopulations could impose additional costs in terms of mortality, with a decreasing

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In this work, we examine patterns of post-fledging and natal dispersal, as well as philopatry of the Chimango Caracara (Milvago chimango) based on band recovery and re-sighting data. The Chimango Caracara is one of the commonest birds of prey in South America. It ranges from Peru, Bolivia, and southern Brazil to Tierra del Fuego in southern Patagonia (Ferguson-Lees and Christie 2001). The species exhibits opportunistic and generalist food habits (Biondi et al. 2005; Baladrón et al. 2009; Josens et al. 2013) that includes facultative scavenging. The Chimango Caracara is a social or solitary species that occupies a variety of environments, including those highly modified by humans (Bellocq et al. 2008; Carrete et al. 2009; Pedrana et al. 2008), and which nests in colonies of different sizes (Solaro and Sarasola 2015). The species has been described as either sedentary, nomadic or partially migratory in the southern part of its distribution (Ferguson-Lees and Christie 2001). However, natal dispersal has not yet been described for this species. We aimed to describe the extent of post-fledging dispersal (i.e. movements within the natal area or excursions outside the natal area during the juvenile stage) and to determine natal dispersal and philopatry of the Chimango Caracara in human modified (suburban), rural and natural habitats of central Argentina.

Materials and methods

Study area

The study was conducted in different habitats in La Pampa Province, central Argentina (Figure 1(a)). From a biogeographical point, our study area was an ecotone between the Pampas and Espinal ecoregions (160-180 m above sea level), dominated by a matrix of agricultural and native forest patches, with an average annual temperature and precipitation of 14-20°C and 400-1000 mm, respectively (Arturi 2006; Viglizzo et al. 2006). Individual Chimango Caracaras were captured and banded in the seven colonies identified in this site that differed among them in the surrounding dominant habitat: three colonies were in suburban habitats, three in rural habitats and one in a nature reserve composed of xerophilous forests, the dominant natural habitat in this region (Figure 1(b)). Although solitary nesting is also known for Chimango Caracaras

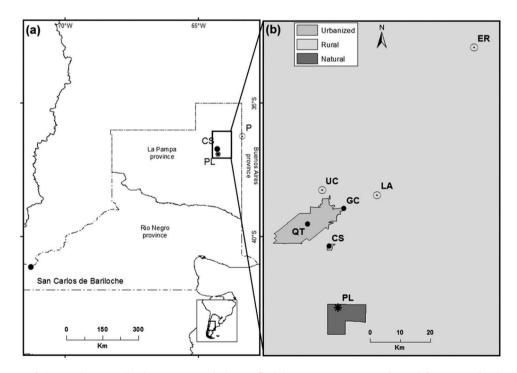


Figure 1. (a) Map of the study area. The longest recorded post-fledgling movement is indicated for one individual from PL in La Pampa Province to P (Pellegrini) in Buenos Aires Province and the longest natal dispersal movement of one individual from CS in La Pampa Province to San Carlos de Bariloche in Rio Negro Province. (b) Sampling sites of Chimango Caracara in La Pampa Province: QT (Quintas Toay), CS (La Cuesta del Sur), GC (Golf Club), LA (La Armonía ranch), ER (El Remanso ranch), UC (campus of the Universidad Nacional de La Pampa), PL (Reserva Natural Parque Luro). Black dots, white dots and black asterisk indicate suburban, rural and natural sampling sites, respectively.

(Fraga and Salvador 1986), in the habitats studied all individuals nested in colonies of different sizes. All the nests were built on shrubs and trees of both exotic and native species.

The suburban areas comprised typical urbanised habitats and were located around the cities of Santa Rosa and Toay. These areas are characterised by a high density of homes and pedestrian and vehicular traffic. These three suburban colonies were located at Quintas Toay (15-30 nests per year, 36.65° S, 64.34° W; QT), La Cuesta del Sur (65-75 nests per year, 36.72° S, 64.27° W; CS) and the Golf Club (8 nests per year, 36.61° S, 64.23° W; GC). Rural habitats in this region included agricultural lands devoted to growing wheat, soybean, sunflower and corn, as well as annual and perennial pastures for livestock with scattered tree stands of exotic tree species, mainly Eucalyptus sp., for cattle shelter. In these areas, human presence and disturbance were lower than in the suburban areas and were usually limited to a single ranch house. These three rural colonies were La Armonía ranch (25-40 nests per year, 36.56° S, 64.13° W; LA), El Remanso ranch (the nesting was not studied, 36.13° S, 63.84° W; ER) and the campus of the Universidad Nacional de La Pampa (3-5 nests per year, 36.56° S, 64.30° W; UC). The colony in natural habitat was located in the Reserva Natural Parque Luro (10-15 nests per year, 36.90° S, 64.25° W; PL), a protected area of 7600 ha designed to preserve the natural Calden (Prosopis caldenia) forest, the dominant tree species in the region. In this study area, human presence was practically nil and limited to park guards.

Bird banding and band recovery

Free-ranging Chimango Caracaras were captured between 2005 and 2015 at breeding colonies by using several trapping methods: walk-in traps baited with meat, bal-chatri traps baited with a mouse and dhogaza nets (Bloom et al. 2007). Nestlings were banded at their nests when approximately 20 days old. All birds were banded with aluminium bands provided by the National Banding Center of Argentina. Individuals were also marked with either patagial tags (Varland et al. 2007) or PVC bands with alpha-numeric codes that enabled identification of individuals in the wild using binoculars, scopes and/or photo cameras. Despite the development of new technologies and the increasing number and diversity of electronic devices that can be applied to the study of animal movements, bird banding remains an important tool to assess the demographics, migration patterns and dispersal movements of birds (Baillie 2001; Newton 2007). While less effective in terms of the time required to recover and gather information than satellite technologies (Bildstein and Peterjohn 2012), bird banding is still a useful methodology for researchers with limited budgets whose aim is to broadly describe movement patterns of birds. For birds of prey, long-term banding and band recovery programmes have permitted the description of dispersal patterns, causes of mortality, migratory routes and timing for several species (Hull *et al.* 2012; Katzner *et al.* 2012; Morrison and Baird 2016).

Captured free-ranging Chimango Caracaras were aged as immature or adult based on plumage characteristics (Ferguson-Lees and Christie 2001) or on external features such as tarsus and cere coloration (Sarasola et al. 2011). A blood sample was taken of each individual for posterior molecular sex identification. For this analysis, we used primers 2550F and 2718R to amplify the W chromosome gene following the procedure of Ellegren (1996). After banding, all birds were released at their capture sites. Only those birds banded as nestlings or captured as fledglings just after the end of the breeding season were considered in our analysis of post-fledgling and natal dispersal. The natal site of these birds was considered as the same as their banding site. Since Chimango Caracaras reach sexual maturity at 2 years of age (see Results), all dispersal movements prior to 2 years post-hatching were considered postfledging movements. Since adult Chimango Caracaras show high breeding site fidelity (Solaro and Sarasola, unpub. data), we considered the encounter site of adult birds during the breeding season to be their final dispersal destination.

During the breeding season from September to December (austral spring) we made an effort to sight banded birds during each visit to the colonies. Encounters of banded birds, through trapping, sightings and reported recoveries, provided data for our determination of post-fledging and natal dispersal events. Occasional encounters of dead birds or reports of banded birds provided by birdwatchers, photographers and rural workers from sites other than the seven breeding colonies we monitored in La Pampa Province were not included in the analyses examining the effects of sex and age of individuals in both post-fledging and natal dispersal distance.

Statistical analysis

We used chi-square tests to assess the independence between natal sites and recapture sites for post-fledging and natal dispersal (i.e. philopatry). Our analyses were done at two scales: habitat and colony. In the first case, which is at a broader scale, we tested whether Chimango Caracaras tend to disperse to sites located in similar or different habitats from those in which they hatched. For this test, we compared the deviation of observed frequencies of Chimango Caracaras that hatched in a certain habitat with the frequencies of those that dispersed to habitats with different degrees of human presence (urbanised, rural and natural habitats). At the second and local scale, we tested whether Chimango Caracaras tend to disperse to similar or different colonies from which they had hatched. In this case, we compared the deviation of observed frequencies of Chimango Caracaras that hatched in four of the studied colonies (in which there was dispersal) with the frequencies of individuals that dispersed to these colonies or to sites where visual sightings were made.

We used generalised linear models (GLMs) with a gamma error distribution and inverse link function (which were the most adequate after exploration of model residuals) to test the effects of sex and age on the dispersal distance of Chimango Caracaras. Sex (male vs. female) and age (immature <2 years old vs. adult >2 years old) were included as covariates to model variation in dispersal distances. For model selection, we started with a model containing both explanatory variables (i.e. the full model) and removed the variable with highest *p*-value (P > 0.05), then proceeded to remove the remaining term. The significance of each variable was tested by comparing the model containing the variable against the new model with the variable removed. Extreme dispersal distances were not

included in the analysis. All statistical tests were performed using program R (R Core Team 2016).

Results

A total of 1738 Chimango Caracaras were banded from 2005 to 2015. Of these birds, 945 were captured and banded as free-ranging immature (<2 years old) or adult birds, and 793 were banded as nestlings (700 birds) or as fledglings (93 birds).

Eighty-four Chimango Caracaras banded as nestlings/fledglings were recaptured or re-sighted either during the post-fledging period (<2 years old; n = 71) or as mature individuals at their breeding sites (n = 13). In addition, 10 of these individuals were successively recaptured both as immatures (during the post-fledgling period) and then as adults at their breeding site, all in the same colony (CS; Table 1; Figure 2). Two individuals (one male and one female) were re-sighted during consecutive years until their first breeding attempts when they were 2 years old. These were the earliest records of Chimango Caracaras attempting to

Table 1. Number of Chimango Caracaras that dispersed different distances (km) during post-fledgling and natal dispersal periods, in La Pampa, Buenos Aires and Río Negro Provinces, Argentina

		Distance (km)						
		•	•	11-		51-	101-	
Period	0	5	10	20	50	100	200	>200
Post-fledgling	62	1	6		1		1	
Natal	18		4					1

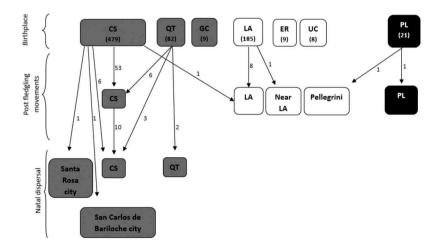


Figure 2. Diagram of post-fledging and natal dispersal of Chimango Caracaras in different areas of the study area in La Pampa Province. Grey, white and black boxes indicate suburban, rural and natural habitats, respectively: CS (La Cuesta del Sur), QT (Quintas Toay), GC (Golf Club), LA (La Armonía ranch), ER (El Remanso ranch), UC (campus of the Universidad Nacional de La Pampa), PL (Reserva Natural Parque Luro). The number of individuals banded at each site is indicated in parentheses and the number of dispersers is indicated to the right of each arrow.

 Table 2. Variation in dispersal distance explained by sex and age of Chimango Caracaras in a generalised linear model

Dependent	Independent			t-	
variable	variable	Estimate	SE	value	Significance
Dispersal	Intercept	0.4633	0.49	0.941	NS
distance	Sex (male)	0.1989	0.67	0.294	NS
	Age (post- fledgling)	0.6111	0.68	0.899	NS

NS: not significant.

breed since no breeding attempts were recorded for birds younger than that age.

The dispersal distance of Chimango Caracaras was not affected by either sex or dispersal stage (Table 2).

Post-fledging dispersal

We were able to determine the post-fledgling dispersal of 71 Chimango Caracaras. Most of these birds (87.3%, 62 individuals) were recaptured at different ages (0–24 months) within the same colony where they hatched. The remaining birds (12.7%, 9 individuals) were recaptured at a median distance of 10 km (median absolute deviation = 0, range = 5–119.2) from their natal site (Table 1; Figures 1 and 2).

During the post-fledgling period, Chimango Caracaras tended to remain in their natal colony or to disperse to habitats with a similar degree of human presence as in their natal habitat (from and towards urbanised habitats) (Table 3; Figure 2).

Natal dispersal and philopatry

We determined the natal dispersal distance of 23 Chimango Caracaras. Most of these (78.2%, 18 individuals) were philopatric, breeding at their natal site. The remaining five individuals (21.7%) were highly variable in their dispersal, travelling a median distance of 10 km (median absolute deviation = 0, range = 9.9-800) (Table 1; Figures 1(a) and 2). The most extreme record was one bird hatched and banded in CS in La Pampa Province in April 2008 and re-sighted as an adult in December 2010 and January 2011 in a suburban area of

Table 3. Results of chi-square tests to assess the independence between natal sites and recapture sites for post-fledging and natal dispersal. Note that natal dispersal at the habitat scale in the analysis could not be determined because all individuals dispersed from and towards urbanised habitats

al	dispersal	ng dispersal Natal dispersal			fledglir	Post-	
ificance	Signific	df	χ ²	Significance	df	χ²	Scale
*	*	3	8.15	***	12	78.22	Colony
-	-	-	-	***	4	95.74	Habitat
		_	-	***	4		

Significance: *** <0.001; * <0.05.

San Carlos de Bariloche, Río Negro Province, Argentina, 800 km away from its natal site (Figure 1(a)).

At the habitat scale, all Chimango Caracaras dispersed from and towards urbanised habitats. At the colony scale, individuals tended to remain and breed in the same colony in which they hatched (Table 3; Figure 2).

Discussion

This study represents the first analysis of the dispersal movements of Chimango Caracaras determining the post-fledgling and natal dispersal distance of individuals living in habitats with different degrees of anthropic perturbation using banding and encounter data. These data permit us to establish that although most individuals can be philopatric, others can disperse long distances from their natal sites. Banding and resighting data also allowed us to confirm that Chimango Caracaras are able to reproduce at a minimum of 2 years of age.

Differences in dispersal distance by sex may be the result of avoiding competition for resources during reproduction (Greenwood and Harvey 1982; Johnson and Gaines 1990). The sex predicted to have the smaller dispersal distances is the sex investing the most to acquire, defend and settle in a vacant site (Forero et al. 2002; Serrano et al. 2003). Thus, the lack of a difference between the sexes in their dispersal distances, such as we found in Chimango Caracaras, could be because the species does not exhibit a marked division of roles during choice and defence of the nesting site (Morrison and Phillips 2000). Moreover, although the small number of colonies in our study area precluded us from analysing the possible effect of colony size, individuals from small or medium-sized colonies seemed to disperse to the larger colony. This could be explained by the conspecific attraction hypothesis, which states that individuals make their dispersal decision based on the presence of, and attraction to, conspecifics (Smith and Peacock 1990; Serrano and Tella 2003; Serrano et al. 2004). However, more studies are needed on sex-biased behavioural patterns in breeding and the possible role of conspecific attraction to explain dispersal dynamics in Chimango Caracara populations.

Re-sightings and band recoveries are limited methodological approaches when aiming to track individual movements. Individuals that were encountered during the post-fledging stage may have moved between different sites until finally settling to breed; such information is lost when using this methodology. Although we had a limited number of encounters, and although individuals likely could have made some movements that we did not detect, all individuals recaptured during both immature and adult stages were located at the same breeding site where they were initially captured. Such a site-dependent recapture probability could indicate that, although during the post-fledging period individuals could explore other potential breeding sites, selection of the breeding site could be made early during the immature stage. In this sense, familiarity with the natal breeding grounds could influence movements of individuals throughout their lives (Green et al. 1989; Forero et al. 2002). According to this idea, a change in the breeding colony would imply a fitness cost that could be avoided if the individuals bred at their natal sites (Serrano and Tella 2012).

During the post-fledging period, most Chimango Caracaras were recaptured in the same place as where they hatched, but some dispersed to sites that ranged between 10 and almost 120 km from their natal site. In terms of natal dispersal, some individuals were philopatric, breeding at the same site at which they hatched, or dispersed a short distance (<10 km) from their natal site. There is, however, an unknown number of individuals that could disperse far away from our study area, as suggested by the report of a long-distance natal dispersal event of one individual travelling 800 km from its natal site and also by the large number of banded birds that were never recaptured or re-sighted. In this sense, our results cannot be considered as conclusive in relation to the general pattern of natal and post-fledging dispersal and the degree of philopatry for the species.

The Chimango Caracara has been described as sedentary, nomadic and even partially migratory, with two distinguishable subspecies: M. c. chimango in central Chile and north-central Argentina and M. c. temucoensis in southern Chile and south-western Argentina. Subspecies differentiation is based only on plumage coloration: M. c. chimango is paler, more cinnamon and more lightly marked than M. c. temucoensis, which is darker brown with bolder markings (Ferguson-Lees and Christie 2001). However, our single report of long-distance natal dispersal indicates that individual birds move between populations of central and south-western Argentina. Although the pattern of plumage coloration of Chimango Caracaras from these regions is described accurately, it could be affected by other factors such as environmental conditions (e.g. temperature and solar radiation) (Ohtsuka et al. 1994; Tran et al. 2008; Galván et al. 2010).

This study represents the first analysis of the dispersal of Chimango Caracaras, based on the most intensive banding effort on a neotropical raptor population to date. Although further studies are needed on whether conspecific attraction affects dispersal, we found that Chimango Caracaras would disperse towards larger colonies, such that they may make their dispersal decision based on the presence of, and attraction to, conspecifics. Lastly, while some individuals were philopatric and bred in the same site where they were born, others could disperse several hundred kilometres to breed. These results have strong implications for demographic patterns, as well as for population dynamics and the genetic structure of Chimango Caracara populations. However, more research is needed to fully understand dispersal patterns in this common raptor which, despite being well adapted to human-altered environments, has been surprisingly poorly studied.

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