Migration routes and stopover sites of Upland Geese *Chloephaga picta* in South America

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ABSTRACT

The Upland Goose (*Chloephaga picta picta*) is a migratory species of South America, which breeds from September to April in Patagonia (Argentina and Chile) and winters from May to September in the southern Pampas (Argentina). Despite some protection in both countries, this species is still persecuted and large numbers are killed by unregulated hunting. Therefore, precise knowledge of their migratory routes is vital to ensure protection of necessary resources and sites throughout the year. We deployed five miniaturised satellite transmitters on adult Upland Geese to gather data about breeding, wintering and stopover sites all along their migratory routes. We aimed to identify important areas in the wintering and breeding grounds through kernel density analyses, and to match these sites along the migration routes with protected areas. Tracked birds exhibited different migration routes and reached different breeding grounds. Two individuals travelled from their wintering grounds in Buenos Aires province to their presumed breeding areas in southern Patagonia. However, we also found different stopover sites from another bird in northern Patagonia, from the ones postulated before, and evidence that some Upland Geese are not large-scale migrants. Our results highlight a considerable amount of plasticity in Upland Geese migratory behaviour. This study represents an essential first step towards identifying important stopover sites along the Upland Geese flyways and it also highlights the lack of protected habitats along most of their migration routes.

Keywords: Argentina, conservation, migration, Patagonia, satellite tracking, waterfowl

1. INTRODUCTION

Thirty-eight species (22%) of waterfowl (ducks, geese, and swans) are under some category of threat as defined by the IUCN Red List (IUCN, 2017). Traditionally, many waterfowl have sustained severe population declines due to wetland habitat loss and fragmentation, especially through drainage for agriculture, and hunting (Weller, 1988; Madsen, 1993). Hunting affects waterfowl population dynamics as a direct result of the birds' harvest, but also as an indirect effect by modifying their distribution and behaviour (Madsen and Fox, 1995) including, in some cases, their migratory routes (Dolman and Sutherland, 2008). Moreover, waterfowl have been intensively exploited all over their distributional range, even on their breeding grounds, not only for their meat but also for their eggs (Boere *et al.*, 2007). Nowadays, human exploitation has been considerably reduced and some species are under protective legislation (e.g. Greenland White-fronted Goose [*Anser albifrons*]; Fox *et al.*, 1998).

The above mentioned issues also apply to the Upland Goose (*Chloephaga picta picta*, Gmelin 1789) which is

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one of the three migratory sheldgeese species of South America. In mainland South America, Upland Goose has a similar migration pattern as the other two species, Ruddy-headed Goose (*C. rubidiceps*, Sclater 1861) and Ashy-headed Goose (*C. poliocephala*, Sclater 1857). They reach and stay in their breeding grounds from the end of August onwards to the end of April in Patagonia (Argentina and Chile) and winter from May to August/September mainly in the southern Pampas (central-east Argentina) (Martin *et al.*, 1986; Blanco *et al.*, 2003; Rumboll *et al.*, 2005; Pedrana *et al.*, 2015). In contrast, the population of the subspecies *Ch. p. leucoptera* is confined to the Malvinas (Falkland) Islands and recognised as sedentary (Summers and Grieve, 1982; Summers and McAdam, 1993).

The southern Pampas, the main wintering habitat of sheldgeese, is one of the most anthropogenically modified regions of South America (Bilenca and Miñarro, 2004). This region is critical for the species' conservation, since they feed on pastures and cereal crops, which results in a conflict with humans (Summers and Grieve, 1982; Martin *et al.*, 1986). Argentina declared all sheldgeese as pests in 1931, claiming that they damage wheat crops and reduce its yield (Pergolani de Costa, 1955). During the migratory season, and especially during winter, these species were killed in large numbers due to unregulated hunting and persecution by farmers (Blanco and de La Balze, 2006; Pedrana *et al.*, 2014). Consequently, the South American continental Upland Goose population has dropped by at least 50% over the past 30 years (IUCN, 2017). Accordingly, Upland Goose continental populations have been listed as 'Vulnerable' by the Argentinian Government (López-Lanús *et al.*, 2008) and hunting has been banned and controlled since 2008, although illegal hunting continues (Blanco *et al.*, 2003; Chebez, 2008). In southern Chile, only the Ruddy-headed Goose was officially classified as endangered in 2007 by the National Strategy for Bird Conservation, while hunting of Upland Goose is allowed in southern Patagonia (10 individuals per excursion) between 1 April and 31 August (Law No. 19473, Ministerio de Agricultura, Chile).

Migration involves moving along regular and seasonal routes twice a year between breeding and wintering grounds, while migration routes are further characterised by a chain of key stopover areas (Myers, 1979). These are sites along the migration routes where birds stop to feed and refill their energy stores, which is often essential for their survival during migration. In essence, stopover sites have been described as ecological bottlenecks for some migrants (Myers, 1979; Newton, 2008). Without access to the energy available from stopover sites, birds would be unable to continue or would need to search for alternative stopover sites to continue their journey (Sutherland, 1998; Newton, 2008). Threats to Upland Goose, for example indiscriminate hunting, may occur all along their distributional range while egg predation happens only in their breeding areas. For sheldgeese from mainland South America, two potential migration routes have been postulated, either based on data from banded individuals (Lucero, 1992; Rumboll *et al.*, 2005) or on questionnaires designed for and distributed amongst farmers and naturalists throughout southern Argentina (Plotnick, 1961; Summers and McAdam, 1993): one route runs across eastern Patagonia along the Atlantic coast, and the second route is more westerly along the foothills of the Andes (Figure 1). Lucero (1992) assumed that the different migratory routes might be associated with the breeding area of the birds. Information about migratory routes and connectivity from a band-return-based approach can be complemented and enhanced with the information provided by the application of miniaturised tracking devices (Bridge *et al.*, 2011). While it is paramount to fully elucidate the Upland Goose migration patterns in order to apply adequate conservation measures and protective legislation, this also ensures that birds can locate the necessary resources and sites during their annual journeys. In this paper, we present the breeding, wintering and stopover sites along the migratory routes of Upland Geese by using satellite telemetry (platform terminal transmitters,

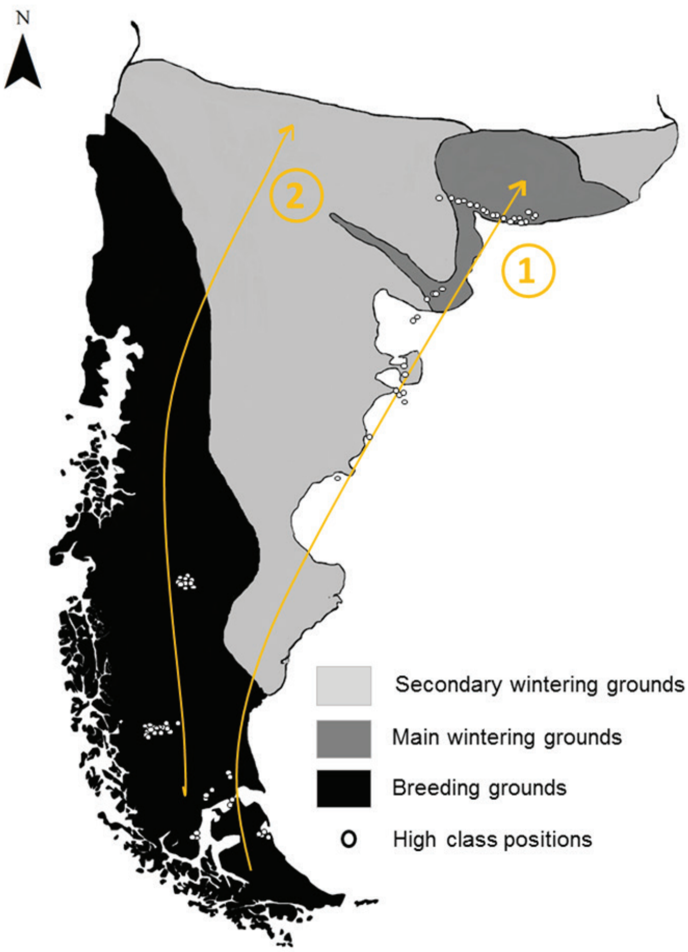

Figure 1 Migration routes of the Upland Goose (*Chloephaga picta*) in South America. Arrows show flight paths: (1) eastern route; and (2) western route (redrawn from Plotnick, 1961; Lucero, 1992; and Summer and McAdam, 1993). White circles are Upland Goose high class positions registered during our study.

PTTs). Satellite tracking is a well-established and effective way to reveal the migration routes and spatial ecology of birds (Jouventin and Weimerskirch, 1990; Nowak *et al.*, 1990; Luukkonen *et al.*, 2008). In this context, we aimed to identify important areas in the wintering and breeding grounds thorough kernel density analyses. In addition, we matched sites used along their migration with protected areas to assess the importance of these sites for the population of Upland Goose and to help in designing future protected areas based on these results.

2. METHODS

2.1 Study area and capture sites

We captured adult Upland Geese in two areas, which are traditionally used by this species for wintering and breeding. One capture area was located in the southern Pampas, Argentina (*i.e.* the southeast of Buenos Aires province) (main wintering grounds; Figure 1), which is an area dominated by pastures and croplands. The other capture area was located on the Brunswick Peninsula at the Agua Fresca River mouth south of Punta Arenas city, which belongs to the Chilean part of Patagonia. Our study area included four Patagonian provinces in Argentina (from North to South: Río Negro, Chubut, Santa Cruz and Tierra del Fuego) and one Chilean region (XII Región de Magallanes y Antártica Chilena) (breeding grounds; Figure 1).The Patagonian landscape is composed of hills and plains whose vegetation cover is dominated by a mixed steppe of grass and shrubs associated with streams, river valleys and wet meadows.

2.2 Satellite tracking data

A total of five satellite tags (battery-powered PTTs, Model K3H179, Kiwisat303, Sirtrack, New Zealand) were deployed on adult Upland Geese. In February 2014, one female Upland Goose (hereafter *Lolita*) was captured by rounding-up a family (male, female and three chicks) in their breeding grounds near Punta Arenas, XII Region de Magallanes y Antártica Chilena. In September 2014, one male (hereafter *Angus*) and, between June and July 2015, three other female Upland Geese (hereafter *Barbara*, *Bjork* and *Berta*) were captured using foot-noose carpets in their wintering grounds near the village of San Francisco de Belloq, Buenos Aires province, Argentina. All birds were equipped with a satellite tag weighing 63 g, attached to their backs using a Teflon harness (Fijn *et al.*, 2012; Humphrey and Avery, 2014). The total mass of instruments deployed on each bird was 76 g, representing less than 3% of the individual's body mass, thus minimising the effects of carrying an additional weight during movements (Kenward, 2001; Phillips *et al.*, 2003; Casper, 2009). We could visually identify the sex of the captured birds because the species shows a strong sexual dimorphism (males: white plumage; females: reddish-brown plumage) (Narosky and Yzurieta, 2010). Individuals were also weighed using a digital balance (precision 0.1 g) and banded with a numbered metal band. The procedure used in this study was assessed and approved by the Chilean Natural Resources of the Agricultural and Livestock Service Agency and by the Buenos Aires Provincial Agency for Sustainable Development (OPDS), Argentina.

Tags were programmed to transmit with a duty cycle of 6 h on/18 h off between 10:00 and 16:00 local time. However, we assumed limited movement within the breeding grounds, and due to the fact that information about departure and arrival dates from wintering to breeding grounds and *vice versa* are scarce (Summers, 1983; Ibarra *et al.*, 2010), we programmed the devices to transmit every day from March to May and from August to October (migration), every two days from June to July (wintering ground), and every three days in 2015 and every seven days in 2016 from November to February (breeding ground). Geographical locations were provided by the Argos service, with location accuracy (class designation) calculated using the Kalman filtering method (Argos, 2016). We only used Argos locations with accuracy classes 0, 1, 2 and 3 (*i.e.* high class positions) for further analysis which accounted for most ($\geq 50\%$) fixes while the other locations with less accurate location classes (A, B, Z) were removed (*i.e.* low class positions). Positional data were then incorporated into a geographical information system and the minimum distance between positions was calculated based on the assumption that the bird travelled in a straight line between two consecutive positions (Table 1).

During migration, geese stop at several sites along the way to rest, refuel or await better weather conditions (Hübner *et al.*, 2010). To identify stopover sites for each individual, groups of continuously tracked positions where the distance between two consecutive positions was not larger than 15 km, *i.e.* the maximum distance between resting and foraging grounds at wintering sites (Pedrana *et al.*, 2015), and where birds remained for at least 48 h within a radius of 15 km, were selected.

2.3 Kernel home-range density maps

For this study, we defined wintering grounds as places used by Upland Geese from May to August inside Buenos Aires province boundaries, stopovers as sites along the migration route between wintering to breeding grounds (spring migration), where birds stayed for a short period of time in a limited area to feed and refill their energy stores, and breeding grounds as sites used by the species from September to April in Patagonia, where birds incubate eggs and raise their chicks. Using this classification, we built density maps for the wintering (Buenos Aires province, Argentina), stopover and breeding grounds (Argentine and Chilean Patagonia). Density maps were generated with kernel home-range utilisation distributions (Worton, 1989). Kernel density analyses have been used effectively to measure habitat use in numerous studies regarding bird species (*e.g.* Copello *et al.*, 2013; Pütz *et al.*, 2016). We used a density function with the smoothing parameter (*h*, *i.e.* search radius) of 15 km and an output cell-size of 1 km, both chosen on the basis of the foraging range of the species and the maximum distance reached (Pedrana *et al.*, 2015). We categorised kernel density areas into three percentile regions corresponding to 50% (the highest density regions or core area), 75% (focal area) and 90% (dispersal area) of the locations (Wood *et al.*, 2000). Finally, we mapped these and all protected areas (*i.e.* natural reserves, national parks, and areas of high value of conservation) together to identify areas of priority to develop a network of protected areas for the species along their flyways. All analyses were performed using R.3.3.1 (package adehabitat), Geospatial Modelling Environment (v. 0.7.2.0) and ArcGIS 10.

3. RESULTS

3.1 Migratory routes and stopover sites

We obtained a total of 3,573 high class positions from the Upland Geese studied (Table 1). On average, birds were tracked for 206 ± 106 (SD) days. Except for *Bjork*, an adult female which was hunted down 49 days after its release, all other birds captured on their wintering grounds stayed until August in their capture area near the village of San Francisco de Belloq, Buenos Aires province, which is an important economical region dominated by crops and pastures (Figure 2a). Then, birds used various migration routes and reached different potential breeding grounds. *Angus* and *Barbara* migrated furthest with a minimum distance of *ca* 1,485 and 1,940 km, respectively, from their wintering grounds in Buenos Aires province to their breeding areas in Patagonia (Table 2; Figure 2a,c).

Angus started its migration on 6 September 2014 and on 21 September reached southern Patagonia (Pedrana *et al.,* 2015; Figure 2a). In these two weeks, *Angus* travelled *ca* 1,189 km while performing four stopovers (Table 2; Figure 2a). The first two stopovers were located in Buenos Aires province (Figure 2b), the third and fourth were located in northern and southern Patagonia, respectively (Figure 2c). The average duration of the stopovers was 5 ± 4 days. Transmissions ceased on 1 January 2015 while the bird was still near El Chaltén, in Santa Cruz province.

Barbara started migrating on 5 August 2015, and by 9 August arrived in southern Patagonia (Table 2; Figure 2a), thus travelling 1,140 km in 5 days while making only one stop for three days near Puerto Madryn, in the Peninsula de Valdés, Chubut province (Table 2; Figure 2b). Four months later, on 17 December 2015, the bird migrated further south (~800 km away from the former site) and reached and stayed on the island of Tierra del Fuego (Table 2, Figure 2c), where transmissions ceased. During this southbound migration, *Barbara* made two stopovers, the first one for a week and the second one for two weeks, in the XII Región de Magallanes y Antártica Chilena, Chile.

Berta's migration route was quite different from that of *Angus* and *Barbara*, since this bird did not head south but travelled east instead (Figure 2a). *Berta* started to migrate on 19 August 2015 and arrived in northern Patagonia, Argentina on November 13 (Table 2; Figure 2b). There it stayed for 73 days until transmissions ceased, only 350 km away from its wintering grounds. During this time, the bird remained at three stopover sites, all of them located close to the coast (Table 2; Figure 2b).

As mentioned above, *Lolita* was the only bird captured on its breeding ground. Unlike all the other birds, she did not migrate during the winter, but remained near her capture area throughout the study period of 342 days. *Lolita* stayed together with a group of conspecifics, which was confirmed by re-sightings following 1, 4 and 90 days after device deployment (Matus, R., personal communication). At the first two re-sightings, *Lolita* was seen together with a male and one gosling, and on the third one within a group of Upland

Table 1 Summary of Upland Geese (*Chloephaga picta*) deployed with satellite transmitters (PTTs). This includes displacement (the sum of all distances the bird travelled in a straight line between two positions), the number of positions received by Argos and the percentage of high class positions (HC)

Upland Geese name	PTT id	Sex	Weight (kg)	Deployment location	Tracking period	Duration (days)	Displacement (km)	Positions received	%HC
Angus	40467	M	3.30	38°37′12″S, 60°04′48″W	01/09/2014–01/01/2015	122	2,486	713	79
Barbara	40466	F	2.60	38°42′18″S, 60°04′19.2″W	30/06/2015–31/03/2016	275	2,789	773	63
Berta	42557	F	2.59	38°41′52.8″S, 60°03′50.4″W	01/07/2015–25/02/2016	240	1,199	601	57
Bjork	40468	F	2.73	38°42′39.6″S, 60°03′25.2″W	01/07/2015–19/08/2015	50	214	120	50
Lolita	42552	F	2.60	53°24′7.2″S, 70°58′58.8″W	11/02/2014–19/01/2015	342	2,545	2,684	79

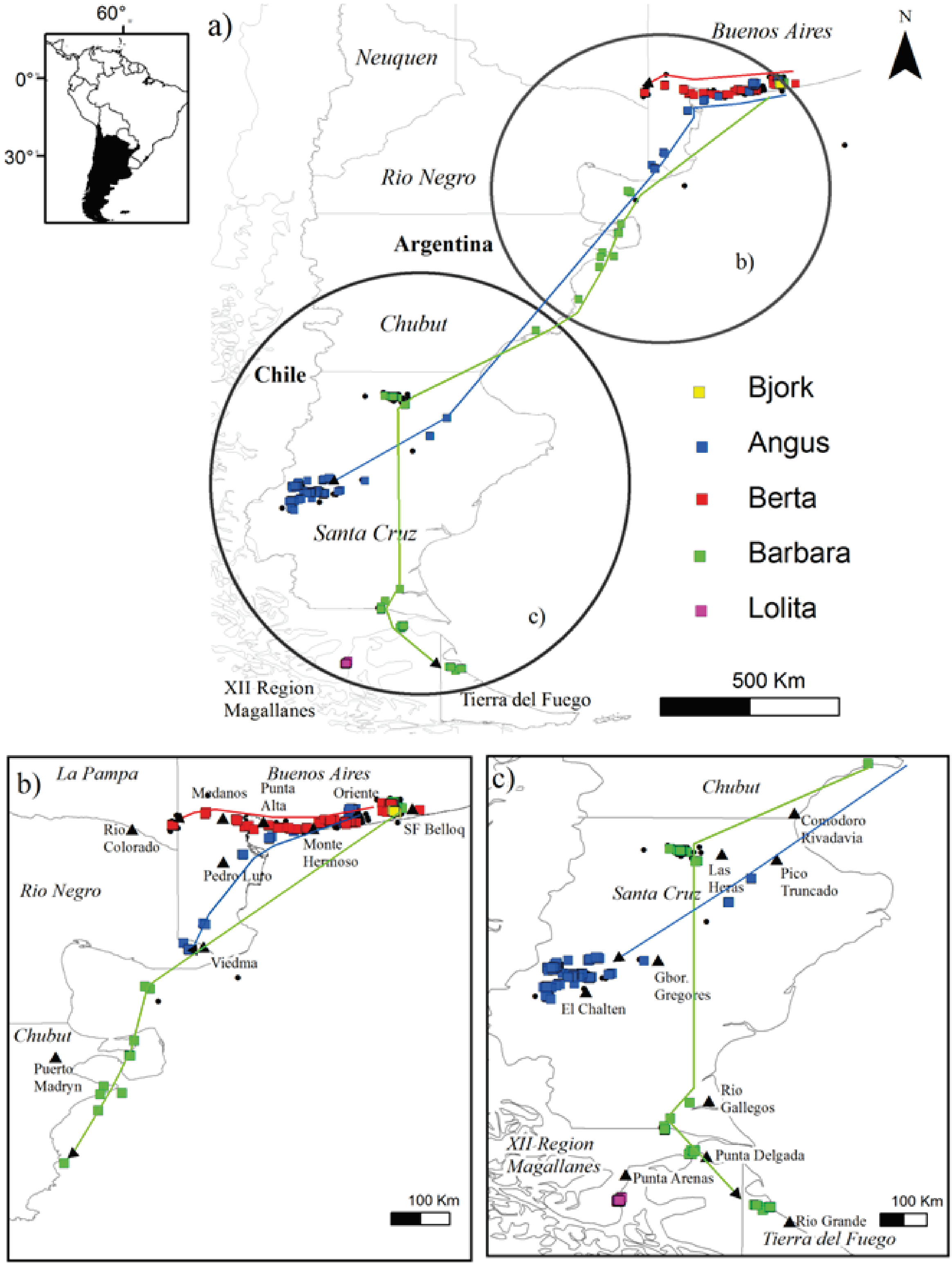

Figure 2 Spring migration routes of Upland Geese (*Chloephaga picta*) from their wintering to their breeding sites, satellite tracked during 2014–2016. Colour squares are high class positions, black dots low class positions, black triangles cities near the stopovers and the colour line is an estimate of the shortest distance between stopovers (see Section 2).

Geese feeding on grasslands. During the breeding season, the bird moved on average 0.76 ± 0.69 km per day, while during the wintering season the bird travelled on average 0.67 ± 0.54 km per day. The longest recorded daily movement was around 13 km.

3.2 Kernel home-range density maps

With the exception of *Lolita*, all other Upland Geese spatially overlapped in Buenos Aires province, with two core distribution areas of 679 km² being identified (*i.e.*

Table 2 Migration routes of Upland Geese *Chloephaga picta* tracked in the wintering, migration and breeding period. Minimum travel distance is the distance the bird travelled in a straight line between two locations and number of days the bird stayed in each location

Upland Geese names	Period	Dates	Nearest Town	Province or Region/ Country	Duration of the stopovers (days)	Min. travel distance between stopovers (km)
Angus	Wintering	01/09/2014	San Francisco de Belloq	Buenos Aires/Argentina	3	–
	Spring Migration	06/09/2014	Oriente	Buenos Aires/Argentina	10	72
		17/09/2014	Pedro Luro	Buenos Aires/Argentina	2	120
		19/09/2014	Viedma	Rio Negro/Argentina	2	180
		21/09/2014	Pico Truncado	Santa Cruz/Argentina	2	817
		23/09/2014	Gbor. Gregores	Santa Cruz/Argentina	10	175
	Breeding	01/10/2014	Chaltén	Santa Cruz/Argentina	92	55
Barbara	Wintering	30/06/2015	San Francisco de Belloq	Buenos Aires/Argentina	35	–
	Spring Migration	05/08/2015	Puerto Madryn	Chubut/Argentina	3	546
		09/08/2015	Las Heras	Santa Cruz/Argentina	132	690
		18/12/2015	Puesto Límite	XII Magallanes/Chile	8	578
	Breeding	25/12/2015	Puerto Progreso	XII Magallanes/Chile	15	62
		08/01/2016	San Sebastián	Tierra del Fuego/Argentina	82	153
Berta	Wintering	01/07/2015	San Francisco de Belloq	Buenos Aires/Argentina	52	–
	Spring Migration	21/08/2015	Oriente	Buenos Aires/Argentina	25	82
		14/09/2015	Monte Hermoso	Buenos Aires/Argentina	23	56
		28/10/2015	Médanos	Buenos Aires/Argentina	2	97
		13/11/2015	Río Colorado	Río Negro/Argentina	73	86

the larger core area of 646 km² and the smallest of 33 km²; Figure 3b). These two core areas were located near the Atlantic coast and only 75 km away from each other (Figure 3b). *Angus* and *Berta* used the same core area near Oriente but stayed there for different time periods and years (for 10 days in 2014 and for one month in 2015, respectively; Table 2 and Figure 3b). All birds together covered a wintering area of *ca* 4,262 km² (dispersal area), while the core area comprised only 16% of the total area.

In Santa Cruz province, the presumed breeding ground, we identified two core areas, one used by *Barbara* located in the north of the province with an area of 550 km², and another used by *Angus* located to the south covering an area of 660 km² (Figure 3a,c). Together, these two birds covered a breeding area of 5,776 km² (dispersal area) (Figure 3c).

The kernel analysis showed that the core area used by *Lolita* throughout the year was 220 km² (Figure 3d). The core area used by this bird during the breeding season overlapped by 75% with the one used during the non-breeding season.

The analysis of distribution in relation to the protected areas indicated that less than 5% of the core areas used by all birds overlapped with a protected area: a small part of *Barbara's* core area overlapped with the Argentinian provincial reserve, 'Costa Atlántica Tierra del Fuego', located in Tierra del Fuego island, and *Lolita's* core area was partly located inside an area designated as Magellanic Strait High Conservation Value Area in Chile (Figure 3d).

4. DISCUSSION

This study presents the first satellite tracking of the migration of Upland Geese between their wintering grounds and breeding grounds. Our results highlight new findings on the migration routes and the spatial ecology of Upland Geese, allowing initial conclusions about goose behaviour such as the timing of migration, stopover sites and time period between stopover staging laps. Also, potentially threatening interactions with human activities could be elucidated by the small overlap between geese habitat and protected areas and by the tracked individual hunted during its migration.

Previous studies on Upland Goose migration postulated two major migration routes in South America: one eastern route and another western route (Figure 1). In addition, Summers and McAdam (1993) proposed that the first one involves a larger proportion of birds which make a long crossing over the Gulfs of San Matías and San Jorge (Argentina; Figure 1). In our study, two individuals, *Barbara* and *Angus*, were in accordance with the proposed eastern route as they migrated in August to September through the southern Buenos Aires province along the Atlantic Coast to reach their first potential breeding grounds in southern Patagonia (Santa Cruz province), although they arrived almost one month apart from each other. Plotnick (1961) postulated that Upland Geese stay in Buenos Aires province until the last days of August when the spring migration starts and that by 20 September most of the geese have left their wintering grounds. Upon arrival

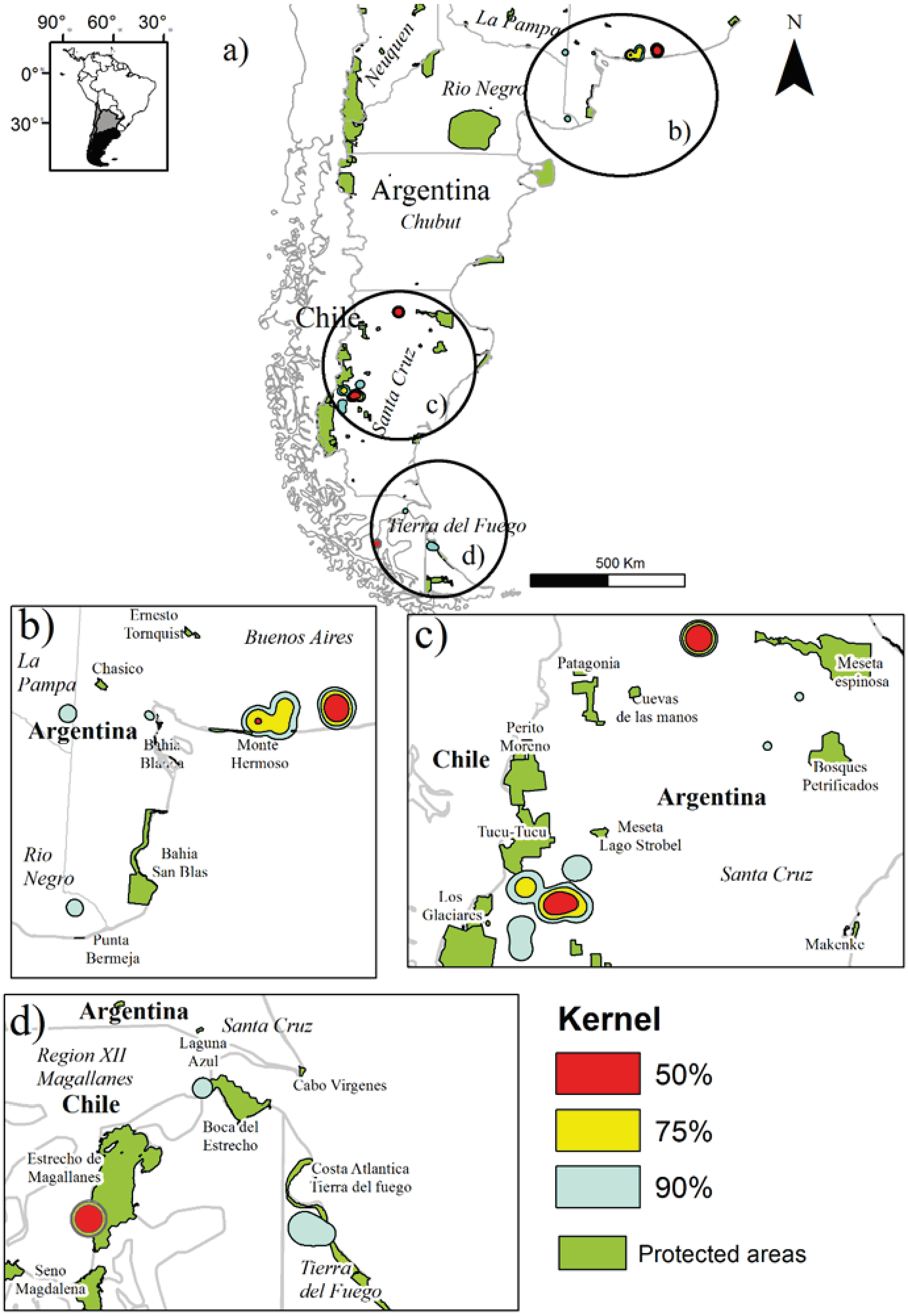

Figure 3 Kernel home-range distribution maps for 50% (core area, red), 75% (focal region, yellow) and 90% (dispersal area, light blue) of Upland Goose (*Chloephaga picta*) and protected areas in Argentina and Chile: (a) All distributional range; (b) wintering grounds; (c) breeding grounds in Santa Cruz province, Argentina; and (d) breeding grounds in XII Región de Magallanes y Antártica Chilena, Chile and Tierra del Fuego province, Argentina.

in their breeding grounds, the incubation period starts between mid-September and October and lasts around 30 days before hatching occurs from the end of October/early November onwards (Summers, 1983). *Barbara* migrated south-eastwards and remained for a period of four months in an area showing very restricted movements, which may be an indication of actual breeding. However, in December the bird continued to migrate around 800 km further south to Tierra del Fuego island. The reasons for this displacement remain speculative. If a breeding attempt occurred further north, the bird may have lost either the clutch or the brood, and was willing to re-lay a second clutch after migrating further south. According to Summers (1983), Upland Geese are able to re-lay a second clutch about 18 days after the first clutch has been lost, although this usually occurs near the original nest. Thus, it appears unlikely that *Barbara* migrated further south in order to lay a replacement clutch. Another possibility would be the loss of her mate. Thus, subsequent movements were performed in order to find a new mate and/or to join a shedding flock, as has also been described by Summers (1983). However, the true reason for this unusual behavioural pattern remains unknown and further research should take into account this behaviour.

In contrast, the migration patterns of two other study birds, *Berta* and *Lolita*, did neither conform to the proposed migration routes nor to the established breeding schedule. *Berta* migrated from the wintering grounds in Buenos Aires province to the east instead of further south and stayed in northern Patagonia, which may indicate some plasticity in their migration behaviour, potentially indicating formerly unknown stopover or breeding sites. Further studies, ideally with a larger number of study birds, are needed to confirm additional migratory routes and potential stopovers or breeding grounds as well as to elucidate whether the stopover sites used in spring and autumn are similar, because unfortunately transmissions ceased before our tracked birds started to return to their wintering areas.

Tracked birds also exhibited plasticity in the timing of their migration since they performed diverse numbers and lengths of stopovers during their annual journey. In agreement with Lucero (1992) and Summers and McAdam (1993), we suggest that the diverse migratory routes and stopovers found in Upland Geese might be a response to different factors which in some cases can act together. Previous studies showed that the selection of any stopover sites by avian migrants depends on a diversity of environmental predictors, such as changes in seasonal food availability and/or the cost related to predation or disturbance risks (*e.g.* from farmers and inter- and intraspecific competition) (Chudzínska *et al*., 2015; Shariati-Najafabadi *et al*., 2016). This would indicate that the selection of stopover sites is not only dependent on the spatio-temporal changes in food availability but is also associated to the costs related to food search, predation and inter- and intraspecific competitions. Furthermore, climate changes have also been suggested as one of the main factors causing differences in the timing of migration and migration distance travelled in birds (Newton, 2008; Møller *et al*., 2010).

In agreement with Carboneras (1993) and Summers and McAdam (1993), our results further indicate that some Upland Geese are partial migrants, because *Lolita* stayed for nearly one year in its breeding ground. The underlying reasons for this behaviour remain unclear, but it may be related to the fact that some areas within the overall distributional range of the species do not show substantial seasonal climate changes and therefore individuals might become progressively more sedentary and revolve their life around their breeding ground. This phenomenon is apparent in the Malvinas (Falkland) Islands, where both, Upland and Ruddy-headed Goose populations, remain within the islands year round, since they encounter sufficient resources around their breeding territories (Summers and McAdam, 1993). However, evidence of genome-wide differentiation confirmed that the Upland Goose found in Argentina and Chile are not only morphologically (Summers and McAdam, 1993) but also genetically different from the Malvinas subspecies (Bulgarella *et al.,* 2014; Kopuchian *et al.,* 2016), which might impact on their migratory behaviour. In addition, some authors described that while most sheldgeese in southern Patagonia start their northward migration around the end of April, there are a few individuals that may overwinter on the breeding grounds (Martin *et al.,* 1986; Summers and McAdam, 1993). It was hypothesised that these birds perform alternate migratory movements, *e.g.* in some years they migrate to other areas while in others they stay in their breeding grounds. Robinson and Warnock (1997) described an alternate migration pattern in shorebirds and waterfowl, which was induced by changes in the amounts of snow, seasonal rainfall and/ or temperature, generating a shifting mosaic of habitats where areas may hold key characteristics of a stopover in some years but not in others. It thus appears that some Upland Geese may encounter enough food and favourable conditions in Patagonia and, as a result, may remain near their breeding territories all year round. By doing so, they may also avoid the threats and hazards encountered during a long-distance migration. For instance, Palacin *et al*. (2016) found that human-induced mortality during migration might be affecting the migratory patterns of Great Bustards (*Otis tarda*), resulting in an increasing number of sedentary individuals over the years. As we pointed out before, the exact reasons why *Lolita* stayed together with some conspecifics in their breeding area for the winter period remain unknown. It appears unlikely however, that the observed behaviour was induced by the equipment with a satellite tag, as *Lolita* was always seen together with other, non-equipped conspecifics over the winter period, indicating that non-migration is more common than previously anticipated. Further research on the migratory patterns of Upland Geese from Patagonia is needed to elucidate whether the observed behaviour is more common than previously thought or just related to exceptional circumstances.

In their wintering grounds, tracked birds mostly used areas overlapping with highly suitable areas demarcated by Pedrana *et al*. (2014), using habitat-suitability maps composed of the most important environmental and anthropogenic predictors. These areas were concentrated in eastern Buenos Aires province far away from urban centres and were mainly characterised by a low elevation terrain interspersed with streams and lakes and a high abundance of crops and pastures for livestock (Pedrana *et al.,* 2014). The correlation between the areas used by our study birds and the ones characterised by Pedrana *et al.* (2014) is not surprising, since the association of these birds with productive grounds and the proximity to waterbodies has been described before for Argentina (Martin *et al.*, 1986; Blanco *et al.*, 2003) and for other species of geese all around the world (Van Der Graaf *et al.*, 2005). Furthermore, we found great overlap between the areas used by *Angus* and *Barbara* and high suitability areas described by Pedrana *et al.* (2011) in southern Patagonia, Argentina, using habitat-suitability maps. Most of the areas used by these birds were located in high or medium suitability areas for sheldgeese occurrence, described as highly productive regions close to mesic habitats, such as streams, rivers and wet meadows and positively correlated with sparsely populated areas (Pedrana *et al.,* 2011). Even though the Upland Goose is perhaps one of the *Chloephaga* species which is less reliant on mesic habitats, as it is also present in dry pastures and arable land for most of the year (Carboneras, 1992); these habitats may be important for the survival and reproduction of this species in the context of a semi-arid Patagonian steppe. In comparison with the others tracked birds, *Lolita* used the same core areas all year round, which might indicate a tendency of the bird to remain faithful to its breeding site throughout the year. The habitat used by this bird during the study period was characterised by grassland clearings in river mouths in the forest/steppe ecotone, where the vegetation is dominated by a mixed steppe of grass and shrubs. As *Angus* and *Barbara*, *Lolita* was associated with high-productive habitats such as areas near wetlands, lakes, and streams. *Lolita*´s selection of such high-productive habitats might have influenced its decision to remain on the same area year around.

To conserve wildlife and preserve endangered or vulnerable species, it is important to protect habitats, regulate hunting, and prevent illegal killing. Cossa *et al.* (2017) highlighted that some of the actions that should have a positive and quick effect on continental sheldgeese population recovery are restoration of breeding sites by controlling introduced carnivores, conserving natural vegetation cover in their breeding grounds and preventing illegal hunting throughout the distribution area. Although hunting of Upland Goose is prohibited in Argentina, and regulated by a hunting law in Chile, there are still several hunting lodges which continue to advertise and promote illegal hunting activities of all three species of migratory sheldgeese (Pedrana, J., personal communication). In accordance, one of our study birds, *Bjork*, was killed within its wintering ground before migration was initiated. Our results indicate that almost all core areas used by the Upland Geese studied were not included in any kind of protection (Figure 3).

To summarise, tracking the migratory routes of Upland Geese using miniaturised tracking devices provided detailed information on birds' movements and habitat use, which can help both ornithologists and managers to design conservation and management strategies (Robinson *et al.*, 2009). In order to develop successful long-term conservation programmes and to apply adequate conservation measures and protective legislation, it is imperative to understand Upland Geese movement patterns, including stopover sites, during their entire annual journey. Furthermore, there is a need to know the spatial (*i.e.* landscape, regional, and continental) and the temporal (*i.e.* within and between seasons and years) variation in ecological context and resources (Mehlman *et al.*, 2005). It will be crucial to gain information about the spatial distribution of environmental and human drivers on the Upland Goose distributional range in order to address threats along the annual journey and to understand the selection of stopover sites in the future.

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