



Movement Patterns of Frugivorous Birds Promote Functional Connectivity among Chaco Serrano Woodland Fragments in Argentina

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ABSTRACT

Movement patterns of frugivorous birds may be altered in anthropogenically fragmented landscapes, with possible consequences for seed dispersal and plant recruitment. We studied the movement patterns and functional connectivity of six frugivorous bird species (*Colaptes melanochloros*, *Thraupis bonariensis*, *Pitangus sulphuratus*, *Saltator aurantiirostris*, *Turdus amaurochalinus*, and *Elaenia* spp.) in a fragmented Chaco-woodland landscape in Argentina. We recorded the directions of bird movements (arrivals and departures) and whether their destination was oriented toward a specific neighboring fragment. We evaluated the movement rates, distance of interpatch movement, and functional connectivity within the landscape for the six bird species. We applied a novel approach, graph theory, to represent bird movement patterns in the landscape and the functional connections among fragments for each bird species. Bird movements were recorded at point-count stations established along the edges of each fragment. The directions of arrival and departure movements from and to neighboring fragments revealed complex movement patterns. However, the destination of bird movements after leaving the focal fragments was usually concentrated on only a few neighboring fragments of different sizes. *Pitangus sulphuratus* and *T. bonariensis* showed larger movement rates and higher functional connectivity (number of graphs and functional area) than the other frugivorous species. The functional connectivity mediated by movement of frugivorous birds may promote seed dispersal of many bird-dispersed plant species. As forest loss and fragmentation of Chaco subtropical forests increase, understanding the pivotal role of mobile links exerted by avian seed dispersers is vital to maintaining and conserving this unique ecosystem.

Abstract in Spanish is available with online material.

Key words: Argentinian Chaco; fragment size; frugivory; movement ecology; movement rates; *Pitangus sulphuratus*; structural connectivity; *Thraupis bonariensis*.

HABITAT LOSS AND FRAGMENTATION ARE THE MAIN ANTHROPOGENIC PROCESSES THREATENING THE BIODIVERSITY AND MAINTENANCE OF ECOSYSTEM FUNCTIONALITY AROUND THE WORLD. In anthropogenically fragmented landscapes, bird species may change their movement patterns and thereby affect ecosystem functionality. Specifically, frugivorous bird species may modify their foraging behavior and movement decisions with important consequences on seed dispersal and plant recruitment in highly fragmented landscapes (Lehouck *et al.* 2009a,b, Pizo & Santos 2011, Uriarte *et al.* 2011).

The ability to move among forest fragments across a non-forest matrix may differ among functional guilds and bird species (Price 2006, Van Houtan *et al.* 2007, Lees & Peres 2009, Ibarra-Macias *et al.* 2010, Neuschulz *et al.* 2012). Certain traits, such as dietary specialization, foraging behavior, body size, and habitat affinity (*e.g.*, forest dependence), may influence bird movements in fragmented landscapes (Lees & Peres 2009, Lehouck *et al.* 2009b, Gillies & St Clair 2010, Ibarra-Macias *et al.* 2010, Yabe *et al.* 2010,

Neuschulz *et al.* 2012). For instance, frugivores, forest specialists, and large-bodied bird species showed the highest movement abilities in a South African fragmented landscape (Neuschulz *et al.* 2012); similarly, birds that can cross the largest gaps among Amazonian forest fragments are medium- to large-bodied species of insectivores, frugivores, and granivores (Lees & Peres 2009).

Landscape configuration (*e.g.*, interpatch distance, structural connectivity, and fragment size) may also influence bird movements in fragmented landscapes. Toucans (Ramphastidae), for example, more frequently visited fragments close to other forest remnants, suggesting that structural connectivity influenced their movements (Graham 2001). In addition, several studies showed that bird movements decreased with isolation and interpatch distances among fragments (Lees & Peres 2009, Yabe *et al.* 2010, Lloyd & Marsden 2011). However, little is known about the effects of fragment size on bird movement patterns. Small forest fragments generally contain fewer resources, which may influence bird movement decisions. Aside from intrinsic traits, extrinsic factors such as food availability, competition, and risk of predation may also influence movement patterns in fragmented landscapes (Lehouck *et al.* 2009b, Yabe *et al.* 2010).

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The pattern of bird movements among fragments provides a measure of functional connectivity, a concept that refers to the degree to which the landscape facilitates or impedes movement of an organism among fragments and explicitly considers the behavioral responses of different organisms to the various landscape elements (Tischendorf & Fahrig 2000, Bélisle 2005). There are many empirical approaches to studying bird functional connectivity, such as field observations of interpatch movements (Magrach *et al.* 2012) or evaluation of gap-crossing capacity (Bélisle 2005, Boscolo *et al.* 2008). Recently, some authors have assessed bird functional connectivity by applying principles of graph theory (Awade & Metzger 2008, Awade *et al.* 2012). A graph theoretical framework regards the landscape as a network in which fragments are represented as nodes linked by inter-patch functional connections (Urban & Keitt 2001, Awade *et al.* 2012). This theoretical approach has important advantages, because it provides valuable information about landscape connectivity; however, it requires detailed empirical data on movement abilities, which remain scarce for most bird species (Urban & Keitt 2001, Awade *et al.* 2012).

Frugivorous bird species are common in fragmented landscapes around the world and may act as ‘mobile links’ promoting not only functional connectivity but also ecological connectivity among forest fragments via seed dispersal (Lundberg & Moberg 2003, Lenz *et al.* 2011, Pizo & Santos 2011). Nevertheless, there is a gap in our knowledge regarding the relationship between landscape configuration and movement patterns for individual frugivorous bird species. Here, we studied the movement patterns of six frugivorous bird species to evaluate their abilities to move in a fragmented landscape of Chaco subtropical woodland and to assess their functional connectivity among fragments. We used field observations on departures and arrivals from and to focal fragments by frugivorous birds, observations that are simple to obtain yet allow for the estimation of functional connectivity among forest fragments at small spatial scales. We also applied a novel approach, graph theory (Awade & Metzger 2008, Awade *et al.* 2012), to represent bird movements in the landscape and the functional connection among fragments promoted by each bird species. Movement patterns were defined by movement rates and the direction and destination of movements to or from different neighboring fragments. We evaluated if the destination of bird movements was oriented toward a neighboring fragment of a particular size or whether movements occurred at random with respect to the availability of forest fragments in the landscape. Also, to determine which bird species would be more able to functionally connect the Chaco woodland fragments, we compared: (1) bird movement rates; (2) distance of interpatch movement; and (3) functional connectivity of fragments visited by six frugivorous bird species.

METHODS

STUDY SITE.—The threatened ecosystem of the Chaco subtropical dry forest has suffered a strong increase in deforestation due to the expansion of agriculture (Gavier & Bucher 2004,

Zak *et al.* 2004), making it an important hotspot of forest loss in Latin America (Aide *et al.* 2012). We selected seven Chaco Serrano woodland (CSW) fragments of different sizes (Fig. S1) that are immersed in an agricultural matrix (soy and corn) in the Santo Domingo farm, located in the Chaco region of the province of Córdoba, Argentina (31°09' S to 31°13' S and 64°13' W to 64°17' W). Mean annual temperature is 16°C, with maxima of 45°C and minima of −9°C (Capitanelli 1979). Most precipitation falls from October to March (on average 750 mm) (Luti *et al.* 1979, Moglia & Gimenez 1998), coinciding with the fruiting peak of bird-dispersed plants. The dry season extends from April to September (on average 116 mm of rainfall), which coincides with the period of low temperatures (Capitanelli 1979). This region is considered semiarid due to the high evaporation rates, which create a water deficit during 11 months of the year (Capitanelli 1979). In addition, the beginning of the rainy season is unpredictable, occurring from September to January.

Fragments are composed of secondary forest with a canopy that usually reaches 7–9 m high (Luti *et al.* 1979, Cabido & Zak 1999). Native vegetation includes numerous bird-dispersed species (Cagnolo *et al.* 2006, Ponce *et al.* 2012, M.C. Díaz Vélez, W.R. Silva and L. Galetto, unpubl. data), the majority of which are trees and shrubs (Table 1), with climbers (*Passiflora morifolia*, *P. suberosa*) and herbs (*Salpichroa origanifolia*, *Solanum chenopodioides*, *Rivina humilis*, *Lantana grisebachii*) being underrepresented. Some exotic bird-dispersed species occur in the fragments, such as *Ligustrum lucidum*, *Morus alba*, and *Lantana camara*.

LANDSCAPE CONFIGURATION.—We used a classified Landsat TM5 satellite image (bands 3, 4, and 5) to calculate interpatch distance, area, and Euclidean nearest-neighbor distance for the seven fragments selected and their neighboring fragments (Table 1; Fig. S1).

TABLE 1. Patch metrics calculated with Fragstats and species richness of bird-dispersed shrubs and trees for the seven Chaco Serrano Woodland focal fragments (see fragments in Fig. S1).

Fragment number	Fragment area (ha)	Euclidean nearest neighbor distance (m)	Richness of bird-dispersed shrubs and trees ^a
1	0.7	81	13
2	1.4	57	14
3	4.1	57	14
4	5.3	64	12
5	13.6	57	17
6	15.1	57	15
7	2493	57	16

^aPlant species: *Berberis ruscifolia*, *Celtis enbrenbergiana*, *Cestrum parqui*, *Condalia buxifolia*, *C. microphylla*, *C. montana*, *Ephedra triandra*, *Jodinia rhombifolia*, *Lantana camara*, *Ligustrum lucidum*, *Litbraea molleoides*, *Lycium cestroides*, *L. ciliatum*, *Morus alba*, *Portieria microphylla*, *Schinus fasciculatus*, *Solanum argentinum*, *Zanthoxylum coco*, and *Ziziphus mistol* (M.C. Díaz Vélez, W.R. Silva and L. Galetto, unpubl. data).

TABLE 2. Characteristics of the six frugivorous bird species studied in the Chaco Serrano Woodland fragmented landscape.

	Bird species					
	<i>Colaptes melanochloros</i>	<i>Thraupis bonariensis</i>	<i>Pitangus sulphuratus</i>	<i>Saltator aurantiirostris</i>	<i>Turdus amaurochalinus</i>	<i>Elaenia</i> spp. (<i>E. albiceps</i> and <i>E. parvirostris</i>)
Family	Picidae	Thraupidae	Tyrannidae	Thraupidae	Turdidae	Tyrannidae
Common name	Green-barred woodpecker	Blue-and-yellow tanager	Great kiskadee	Golden-billed saltator	Creamy-bellied thrush	Elaenia
Body size(cm) ^a	23	17	22	12	21	13–15
Body mass (g) ^b	127	36	67	42	65	17

^aData obtained from Narosky and Yzurieta (2010).

^bData obtained from Del hoyo *et al.* (2002), Montaldo (2005), and Dunning (2007).

We categorized land cover into only two classes, *forest* and *non-forest*, because all fragments in the study region consisted of second-growth CSW and the landscape matrix is formed mainly of open agricultural habitat. We used the software Fragstats (McGarigal *et al.* 2002) to calculate area and Euclidean nearest-neighbor distance of the fragments.

FRUGIVOROUS BIRD SPECIES STUDIED.—We selected six species (Table 2): *Colaptes melanochloros* (Green-barred Woodpecker), *Thraupis bonariensis* (Blue-and-yellow Tanager), *Pitangus sulphuratus* (Great Kiskadee), *Saltator aurantiirostris* (Golden-billed Saltator), *Turdus amaurochalinus* (Creamy-bellied Thrush), and *Elaenia* spp. (includes *E. parvirostris* and *E. albiceps*). These are important seed dispersers as they are among the most common species in the study area and because they include a high proportion of fruit in their diet (M.C. Díaz Vélez, W.R. Silva and L. Galetto, unpubl. data, Caziani 1996, Montaldo 2005, Francisco *et al.* 2007). The generic and specific names of bird species follow Remsen *et al.* (2012).

BIRD MOVEMENT OBSERVATIONS.—During the peak of fruit production of bird-dispersed plant species (January and February 2010), we recorded bird movements during 6 to 11 observation sessions for each fragment (focal fragments hereafter, Table 3). In each session, the observer stayed at a variable number of 10-min unlimited-distance point-count stations, which we established near the edges of each focal fragment (Table 3). For each bird movement detected during the 10-min point-count, we recorded: bird species, number of individuals departing from or arriving at the focal fragment and, whenever possible, the neighboring fragment to which the birds headed or from which they arrived. Considering that each individual can move seeds among forest fragments independently of its flock partners, when we observed a flock of the same bird species, we counted each individual separately to calculate movement rates. Observation sessions began at sunrise and ended within 4 h. We established each point-count station in the matrix (soy or corn) at a distance of 15 m from the edge of the focal fragments. The number of point-count stations and the distance between them (50–100 m) varied according to fragment size to cover the entire perimeter of the fragment (Table 3). All

but the largest fragment had six observation sessions during the season to account for temporal variability in fruit availability and bird activity (Table 3). We regularly changed the location of point-count stations during each observation session.

DATA ANALYSIS

DIRECTION AND DESTINATION OF BIRD MOVEMENTS.—We used bird movement data with known arrivals and departures to evaluate the directions (*i.e.*, arrival and departures to and from focal fragments) and destination (only departures from the focal fragments) among the seven focal fragments. For approximately, 55 percent of the bird movements recorded, we could identify the neighboring fragment that the birds flew to or departed from.

To evaluate whether the destination of bird movements after leaving the focal fragment—*i.e.*, only bird departures—occurred at random with respect to the availability of the different sizes of neighboring fragments, we used the technique proposed by Neu *et al.* (1974). This technique uses a Bonferroni χ statistic to calculate simultaneous confidence intervals based on observed frequencies of flight destinations that are contrasted with expected frequencies calculated according to the availability of the

TABLE 3. Number of observation sessions (OS), number of 10-min unlimited-distance point-counts (PC), and total number of PC for each Chaco Serrano Woodland focal fragment (see fragment location within the landscape in Fig. S1).

Fragment number	N° of OS	N° of PC per OS	Total number of PC
1	6	5	30
2	6	5	30
3	6	10	60
4	6	10	60
5	6	20	120
6	6	20	120
7	11	20–30	242

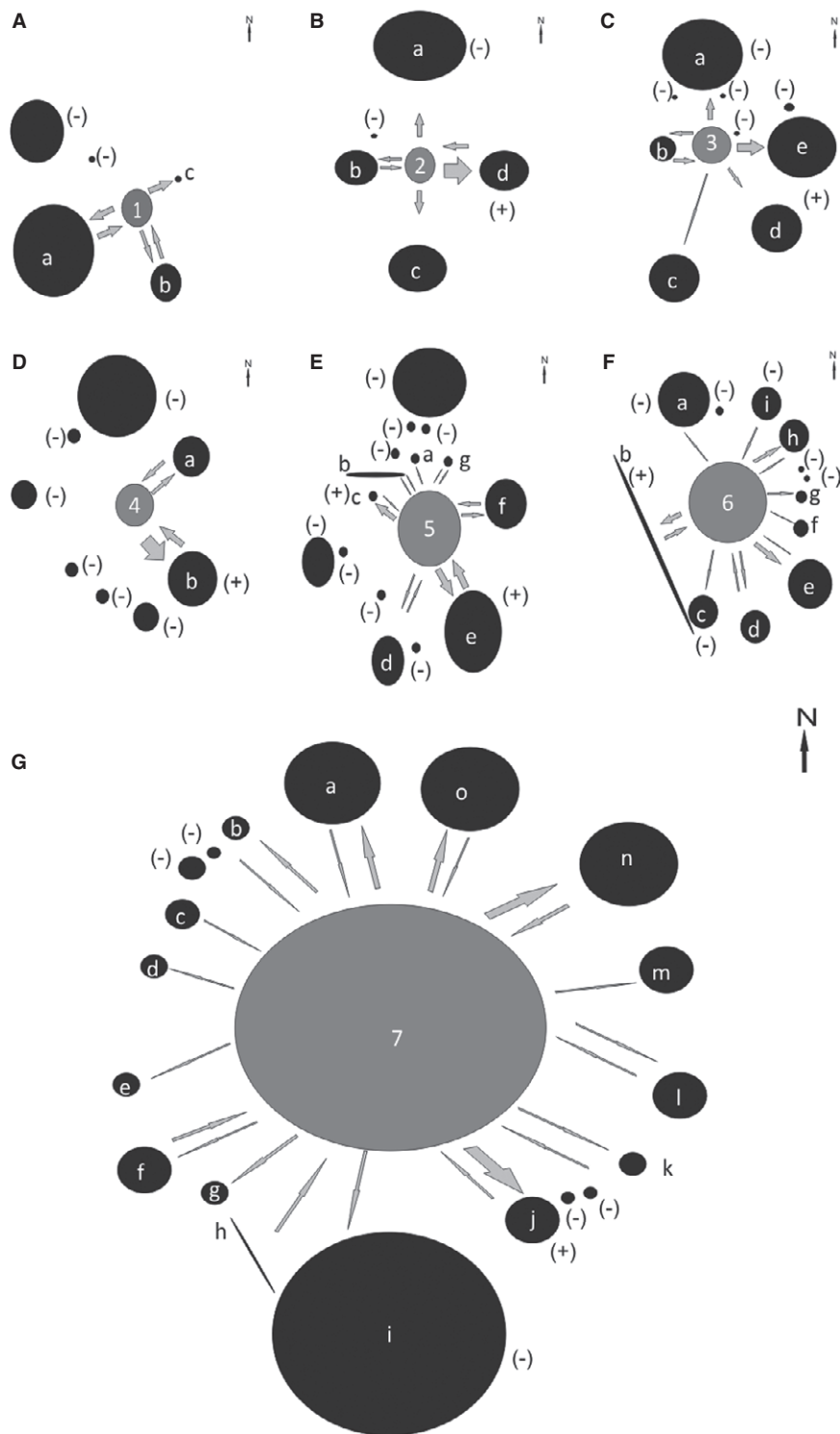


FIGURE 1. Diagrams of the seven focal fragments in gray with focal fragment number: (A) 1, (B) 2, (C) 3, (D) 4, (E) 5, (F) 6 and (G) 8 (see Table 1 for more details of fragment characteristics) and the neighboring fragments (circles correspond to fragments and lines refer to live fences, all in black). Arrows of different width indicate the proportion of bird interpatch arrivals and departures at or from each neighboring fragment recorded in the point-count stations (see Table S2 for more details of neighboring fragments denoted by letters). The signs in parentheses next to each neighboring fragment indicate whether a given destination (only for bird departures from the focal fragments) is more (+) or less (-) frequent than expected based on the area covered by the fragments. Neighboring fragments without signs denote bird visits proportional to their area (see Methods section for details of calculation of Confidence Intervals). Fragment sizes and distances among fragments are proportional to real sizes and distances in the fragmented landscape.

neighboring fragments given by the areas they cover (Neu *et al.* 1974, Pizo & Santos 2011).

BIRD MOVEMENT RATES AND DISTANCE OF INTERPATCH MOVEMENTS.—Based on the 662 10-min point-counts, we calculated the movement rates for each bird species (number of bird movements per hour) by sampling day (32 days). We calculated interpatch distances for each bird species using the satellite image of the landscape (a classified Landsat TM5 satellite image). We examined the differences in movement rates and distance of interpatch movements among the six bird species using the non-parametric Kruskal–Wallis test and *a posteriori* median test, as values were not normal or homoscedastic.

FUNCTIONAL CONNECTIVITY.—We used the movement data with known arrivals and departures to calculate the functional connection among fragments for each bird species using graph theory, following Awade and Metzger (2008). A graph consisted of a group of nodes (*i.e.*, the fragments) connected by edges (*i.e.*, interpatch movements). We considered that two fragments were connected if we were able to record bird movements between them. The sum of the areas of the fragments belonging to the same graph is the graph area or functional area, and it was considered as a functional connectivity measure (Awade & Metzger 2008).

RESULTS

We recorded a total of 883 bird movements from or to each of the seven focal fragments in 662 point-counts totaling 110 h of observation. In 31 percent of the bird movements, we could not identify the bird species. Eleven percent of the recorded bird movements involved non-frugivorous bird species, whereas 54 percent of the movements involved the six selected frugivorous bird species, and only 4 percent involved other frugivorous bird species.

DIRECTION AND DESTINATION OF BIRD MOVEMENTS.—We recorded more bird movements from focal fragments to neighboring fragments than vice versa (Fig. 1, see Table S1 for more details). In the smallest focal fragments, we found the highest proportion of bird movements from or to larger neighboring fragments (Fig. 1A and B). In medium-sized focal fragments, the highest proportion of bird movements was also to or from neighboring fragments with a larger or similar area (Fig. 1C and D). Finally, in the largest focal fragments, bird arrivals and departures were not concentrated in a particular fragment area; instead, they were spread between available neighboring fragments of similar or smaller areas (Fig. 1E–G).

Pitangus sulphuratus and *T. bonariensis* accounted for most of the bird departures from and arrivals to focal fragments (see Table S1 for more details; except for the 5.28 ha fragment where *P. sulphuratus* was not recorded). Movements of *Elaenia* individuals to or from neighboring fragments were recorded in almost all the focal fragments, but accounted for a small proportion of the movements relative to the other bird species (Table S1). *Turdus*

amaurochalinus, *S. aurantiostris* and *C. melanochloros* departures and arrivals were recorded only in some focal fragments of different sizes (Table S1).

In small- and medium-sized (0.7–5.3 ha) focal fragments, the destination of frugivorous birds did not occur at random, because they were concentrated in a larger (from 4 to 14 ha, Fig. 1B–D), yet not the largest neighboring fragment (2493 ha, Fig. 1B–D). Moreover, the largest neighboring fragment was less visited than expected by chance (Fig. 1B–D). Conversely, for two larger focal fragments, the destination of bird movements was concentrated in neighboring fragments with similar or smaller areas (Fig. 1E and F). Generally, the smallest neighboring fragments were visited less than expected by chance (Fig. 1A–G).

BIRD MOVEMENT RATES AND DISTANCE OF INTERPATCH MOVEMENTS.—Bird movement rates significantly differed among the six bird species ($H = 124.24$, $P < 0.0001$, Fig. 2), being significantly higher for *T. bonariensis* and *P. sulphuratus* than for the other species (Fig. 2). Both species generally moved in conspecific flocks of two to five individuals.

The minimal distance recorded for interpatch movements was 26 m for *Elaenia* spp. and *T. bonariensis*, whereas the maximum distance was almost 400 m for *T. bonariensis*. Notwithstanding, the six species showed similar distances of bird interpatch movements

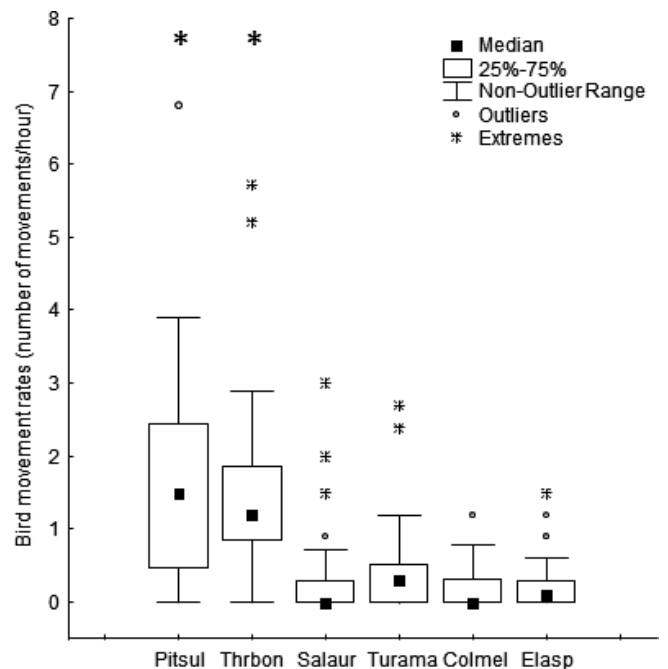


FIGURE 2. Bird movement rates (number of movements per hour) recorded during the 662 point-counts in 32 sampling days (4 h per day) for the six frugivorous bird species. Abbreviations: Pitsul: *Pitangus sulphuratus*; Thrbon: *Thraupis bonariensis*; Salaur: *Saltator aurantiostris*; Turama: *Turdus amaurochalinus*; Colmel: *Colaptes melanochloros*; and Elasp: *Elaenia parvirostris* and *E. albiceps*. *indicates significant differences at $P \leq 0.05$, *posteriori* median test of Kruskal–Wallis.

($H = 5.81$, $P = 0.325$, Fig. 3). The interpatch distance was highly variable for *P. sulphuratus*, *C. melanocloros*, and *T. bonariensis*, which exhibited the maximum distances of interpatch movement (Fig. 3).

FUNCTIONAL CONNECTIVITY.—Functional connectivity varied among the six frugivorous species (Fig. 4). *Pitangus sulphuratus* and *T. bonariensis* presented the fewest graphs and the highest functional areas (Fig. 4A and B), which indicates a high functional connectivity mediated by these two species.

DISCUSSION

DIRECTION AND DESTINATION OF BIRD MOVEMENTS.—We found complex frugivorous bird movement patterns in the CSW fragmented landscape. In general, we did not find a common pattern for the directions of bird departures and arrivals from focal fragments, but the destinations of bird movements from several focal fragments were not randomly distributed across the different neighboring fragments. In small- and medium-sized fragments, bird departures were concentrated in larger neighboring fragments, possibly because these fragments offer more fruit resources to frugivorous birds. Accordingly, Price *et al.* (1999) suggested that the frequency of visitation of mobile frugivores to forest fragments is positively related to fragment size, since larger fragments can offer more fruit resources. Aside from size, other features of neighboring fragments may determine the interpatch movement patterns of the frugivorous birds, such as the struc-

tural complexity of vegetation, forest cover, and the availability and distribution of fruit resources (García *et al.* 2010, 2013, Uriarte *et al.* 2011). Therefore, in a landscape formed by different-sized forest fragments, we cannot expect random exchanges of seeds among fragments mediated by frugivorous birds.

Pitangus sulphuratus and *T. bonariensis* accounted for most of the movements from or to neighboring fragments. Only in larger focal fragments did we record interpatch movements of other frugivorous species. Even though the bird species recorded are all common in the disturbed areas, and are likely among the most common bird visitors to ornithocorous plants in the fragmented landscapes (Pizo 2004, 2007, Gabriel 2005, Pizo & Santos 2011, Magrach *et al.* 2012), only a subset of them make frequent interpatch movements. These species represent the mobile links promoting ecological connectivity among fragments, and plant populations rely on this connectivity to move genes throughout the landscape.

BIRD MOVEMENT RATES AND DISTANCE OF INTERPATCH MOVEMENTS.—*Pitangus sulphuratus* and *T. bonariensis* showed higher movement rates compared to other bird species, generally moving in conspecific flocks. Flocking behavior can explain their high movement rates, because when a flock was observed, each individual was counted to calculate movement rates. Several *Thraupis* species are active frugivores that can move among different types of degraded vegetation (Pizo 2004, Gabriel 2005, Pizo & Santos 2011). *Thraupis sayaca*, for instance, is a key mobile link in several fragmented agricultural landscapes, consuming a considerable number of fruit species with a high plant-visiting rate and connecting several landscape elements through its seed dispersal services (Pizo 2004, Gabriel 2005, Pizo & Santos 2011). *Pitangus sulphuratus* is also a generalist frugivore using many landscape elements, from pastures, live fences, and isolated trees to forest fragments (Pizo 2004, 2007, Gabriel 2005). Remarkably, *P. sulphuratus* and *T. bonariensis* are also important frugivores in the studied Chaco landscape, consuming most of the fruit species growing in forest fragments (Ponce *et al.* 2012, M.C. Díaz Vélez, W.R. Silva and L. Galetto, unpubl. data). By contrast, in other degraded and conserved Chaco forests of Argentina, *E. parvirostris* and *T. amaurochalinus* are the most common frugivorous birds (Caziani 1996, Codesido & Bilenca 2004). Previous studies report *T. amaurochalinus* as one of the main seed dispersers in a conserved Chaco forest of Argentina (Caziani 1996, Codesido & Bilenca 2004) and in several other fragmented landscapes, being a frequent plant visitor across a broad range of habitats (Pizo 2007, Gasperin & Pizo 2009). Several species of *Elaenia* are also important frugivores in many fragmented landscapes and in conserved forests due to their high abundance, fruit-handling techniques, and high fruit consumption rate (Pizo 2007, Magrach *et al.* 2012). Unexpectedly, we found that *Elaenia* spp. and *T. amaurochalinus* showed lower movement rates in this Chaco fragmented landscape, which, in the case of *T. amaurochalinus*, may have to do with its scarcity in the Chaco fragments (M.C. Díaz Vélez, W.R. Silva and L. Galetto, unpubl. data). Despite being abundant at the study site (M.C. Díaz Vélez, W.R. Silva and L. Galetto, unpubl. data),

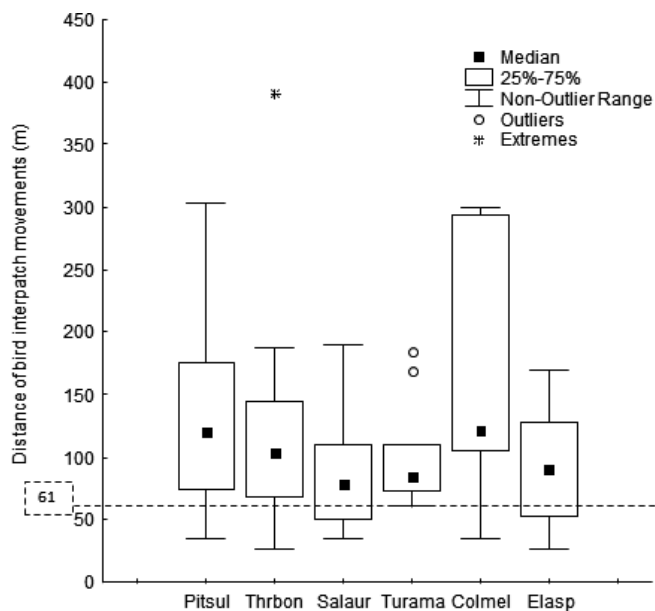


FIGURE 3. Distances of bird interpatch movements covered by six frugivorous birds. Abbreviations: Pitsul: *Pitangus sulphuratus*; Thrbon: *Thraupis bonariensis*; Salaur: *Saltator aurantirostris*; Turama: *Turdus amaurochalinus*; Colmel: *Colaptes melanocloros*; and Elasp: *Elaenia parvirostris* and *E. albiceps*. The dotted line indicates the Euclidean nearest-neighbor mean distance in the fragmented landscape: 61 m.

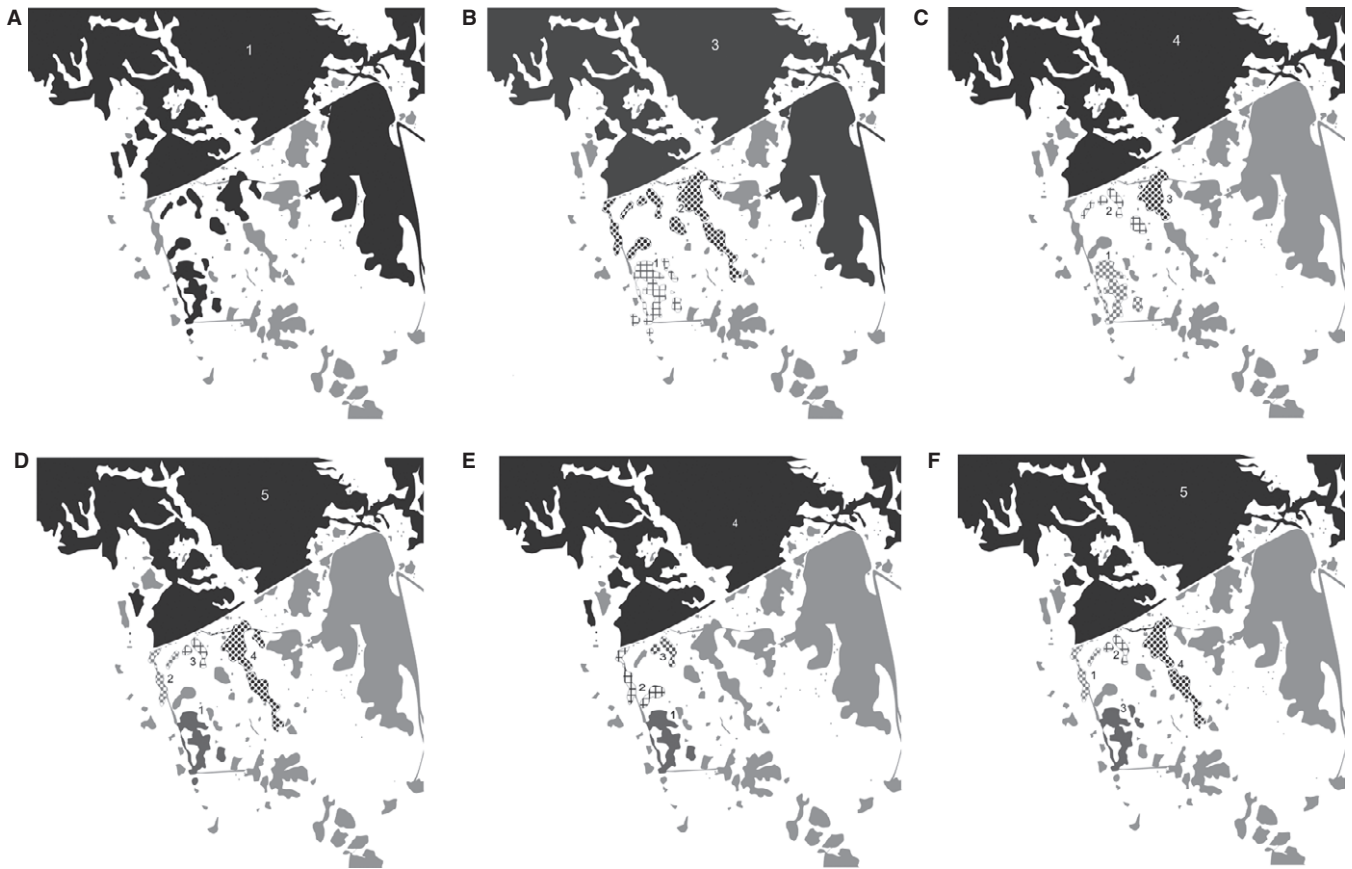


FIGURE 4. Graphs derived from interpatch movements of the six bird species recorded in the point-counts set around the edge of the seven focal fragments: (A) *Pitangus sulphuratus*; (B) *Thraupis bonariensis*; (C) *Saltator aurantiirostris*; (D) *Turdus amaurochalinus*; (E) *Colaptes melanochloros*; and (F) *Elaenia* spp. Each group of fragments of the same color or hatching pattern is a 'graph', and the sum of the areas of the patches belonging to the same graph is the functional area or 'graph area' and is considered as a functional connectivity measurement. Graph area (hectares): (A) 1. 3164; (B) 1. 21, 2. 46, 3. 3106; (C) 1. 17, 2. 10, 3. 14, 4. 2493; (D) 1. 18, 2. 7, 3. 5, 4. 26, 5. 2502; (E) 1. 17, 2. 10, 3. 5, 4. 2499; (F) 1. 7, 2. 5, 3. 17, 4. 23, 5. 2502.

E. parvirostris and *E. albiceps* probably have different foraging decisions and prefer searching for fruits inside fragments rather than among fragments. Magrath *et al.* (2012) observed a similar pattern for *E. albiceps*, which had limited movements according to the distance between fragments and matrix type in a Chilean fragmented landscape. Indeed, Pizo and Santos (2011) found that *E. flavogaster* only moved to isolated trees in pastures if they were within 20 m of the departure fragment. Finally, the low movement rates observed for *C. melanochloros* and *S. aurantiirostris* could have been a consequence of their low abundance in the forest fragments (M.C. Díaz Vélez, W.R. Silva and L. Galetto, unpubl. data). *Colaptes melanochloros* is a semi-dependent forest species (Yabe *et al.* 2010) that may need forest corridors, even as thin as live fences, to move among fragments in search of food (Gabriel 2005). The same could be true for *S. aurantiirostris*, a species closely related to *S. similis*, for which the use of live fences was observed in Brazil (Gabriel 2005).

The distance of bird interpatch movement did not vary among the six frugivorous species. However, we observed maximum distances of interpatch movements for *P. sulphuratus*, *C. mel-*

anochloros, and *T. bonariensis*. The first two species have the greatest body mass among the studied birds (Table 2), which may be related to a better capacity to fly long distances between fragments (Lees & Peres 2009, Yabe 2009).

Variations in movement rates and distances of bird interpatch movements among frugivore species may also be explained by other ecological traits, such as differences in mortality risk in the agricultural matrix (Tischendorf & Fahrig 2000). It is also possible that differences in species detection probabilities could have affected the movement rates and interpatch distances recorded. In fact, smaller and less conspicuous species, like *Elaenia* spp., may have lower detection probabilities than the other bird species.

FUNCTIONAL CONNECTIVITY.—We found that all six bird species can functionally link the neighboring fragments with the focal fragments, but that *P. sulphuratus* and *T. bonariensis* can promote higher functional connectivity due to their higher movement rates and flying orientations to diverse neighboring fragments. The other bird species also have the potential to functionally connect

all the fragments, but more empirical data comparing different landscape configurations are needed to test this idea. We are aware that the spatial scale examined was probably too small, since birds may have the potential to move over larger interpatch distances than those recorded in this study. Furthermore, the movement patterns of frugivorous birds and their consequences on the functional connectivity of forest fragments may change according to the spatial scale considered (García & Ortiz-Pulido 2004, García & Chacoff 2007). In future studies, it would be desirable to use a multi-scale approach to evaluate frugivore movement patterns and changes in functional connectivity in diverse fragmented landscapes.

CONCLUSIONS

The six frugivorous bird species studied functionally connect CSW fragments through their movement patterns, but *P. sulphuratus* and *T. bonariensis* promote higher functional connectivity. Our findings emphasize the importance of comparing movement patterns among diverse frugivorous bird species, because they can respond differently to landscape fragmentation. This is the first study that evaluates the movement patterns of frugivorous birds in a CSW fragmented landscape and it underlines the importance of landscape configuration, such as the presence of small fragments between larger fragments and small interpatch distances, for the maintenance of functional connectivity in the landscape. Moreover, it is important to use novel and complementary approaches, like graph theory and direct interpatch movement observations, to elucidate the functional connectivity promoted by the different bird species in fragmented landscapes. If we translate this functional connectivity into ecological connectivity through seed dispersal, we should consider that all the frugivores, and especially *P. sulphuratus* and *T. bonariensis*, may have important roles in promoting seed dispersal services and, subsequently, the gene flow among populations of many bird-dispersed plant species in CSW fragments. Nevertheless, we are aware that the bird movement patterns described here are indirect measurements of seed dispersal among fragments. For future studies, we suggest linking the bird movement patterns with measurements of efficiency in seed dispersal among the fragments, to also evaluate ecological connectivity in the fragmented landscape (Pizo & Santos 2011, Côrtes & Uriarte 2013 and references therein). As forest loss and fragmentation of Chaco subtropical forests increase, understanding the pivotal role of mobile links exerted by avian seed dispersers is vital for maintaining and conserving this unique ecosystem in South America.

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SUPPORTING INFORMATION

Additional Supporting Information may be found with online material:

FIGURE S1. Spatial location of the studied sites in the Chaco Serrano Woodland of Córdoba, Argentina.

TABLE S1. Proportions of bird movements of each frugivorous bird species to or from neighboring fragments recorded in the seven focal fragments of Chaco Serrano Woodland.

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