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Behavioral plasticity of a threatened parrot in human-modified landscapes

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A B S T R A C T

Behavioral plasticity is a strategy employed by many species to cope with both naturally occurring and human-mediated environmental variability. Such plasticity may be especially important for long-lived and wide-ranging species, such as parrots, that likely face great temporal and spatial variation within their long lifespans, and are often disproportionately affected by anthropogenic habitat change. We used radio-telemetry and roost counts to assess ranging patterns, habitat usage, and roosting behaviors of the Yellow-naped Amazon (Amazona auropalliata) at two sites in northern Costa Rica with different degrees of anthropogenic habitat alteration. We compared behaviors for residents at the two sites and for experimentally translocated individuals to test the hypothesis that this species would employ behavioral plasticity in response to habitat differences. We found that individuals in the region with dispersed vegetation recorded ranging movements and communal roosting behavior ten times larger than the region with concentrated vegetation. Translocated individuals showed flexibility in these behaviors and matched the behavioral patterns of resident birds at the release site rather than maintaining behaviors characteristic of their capture site. Our results illustrate a generalized rapid plastic response to human-induced changes in habitat for a number of behavioral traits in the Yellow-naped Amazon. Such plasticity is directly relevant to reintroduction efforts that are commonly employed as a conservation tool in parrots. Our study provides an example of how behavioral plasticity may allow some wild populations to withstand anthropogenic change.

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1. Introduction

Variability in resource availability is widely recognized as a factor affecting the movement patterns and habitat preferences of animals. Food resources, such as fruits, may show temporal and spatial fluctuations in abundance within and among different habitats (Blake and Loiselle, 1991; Karr, 1976; Levey, 1988; Renton, 2001). Animals may respond to these fluctuations through behavioral plasticity such as seasonal movements (Levey, 1988; Levey and Stiles, 1992; Loiselle and Blake, 1991), modification of local movements (Renton, 2001; Rey, 1995; Saracco et al., 2004), diet switching (Galetti and Pedroni, 1994; Gautier-Hion, 1980), or social living strategies (Richner and Heeb, 1995; Ward and Zahavi, 1973). The influence of food resource fluctuations in animal movement is so profound that it has been suggested as an evolutionary factor predisposing Neotropical birds to perform long-distance migrations (Levey and Stiles, 1992).

Understanding the response of animals to resource fluctuations has taken on a new urgency with the pervasive and severe changes in the environment caused by human activities. Species may differ in the degree and rapidity with which they are able to modify their behaviors when facing human-induced changes in the environment (Tuomainen and Candolin, 2011; Visser, 2008). Some species may exhibit a high degree of plasticity in the phenology of life history traits and distribution range when facing new environmental conditions (Crozier et al., 2008; Tuomainen and Candolin, 2011; Walther et al., 2002). Conversely, in other cases animals may lack a plastic response to environmental changes, causing a mismatch between a species' traits and the new conditions (Both et al., 2006; Edwards and Richardson, 2004). While behavioral plasticity is normally expected to positively impact fitness, this response may sometimes be maladaptive. An example of this maladaptive behavior are ecological traps, in which individuals use human-modified habitats that appear to be high-quality but are in fact low-quality in function (Robertson and Hutto, 2007). The degree to which animals can adapt to anthropogenic change may be determined in part by the degree to which they are plastic in their behavioral responses to historic environmental variability.

Parrots (Order Psittaciformes) are social birds with a largely tropical distribution (Forshaw, 1989) and a high degree of conservation concern (Snyder et al., 2000). They are seed predators that typically range over large areas to locate fruits and seeds that are

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heterogeneously distributed in space and time (Renton, 2001). As such, their behavior likely reflects adaptations for responding to fluctuations in resource distributions. Previous research in both Neotropical and Australasian parrots (Ortíz-Maciel et al., 2010; Salinas-Melgoza, 2003; Saunders, 1980, 1990) indicates that low resource environments may trigger an increase in the magnitude of their movements. Many species, both invasive and native, will also use human-altered landscapes and the resources available therein for foraging, roosting, and nesting (Eberhard, 1998; Manning et al., 2009; Manning and Lindenmayer, 2009; Nally and Horrocks, 2000; Saunders, 1980, 1990). These traits may predispose parrots to exhibit flexibility in their behavioral response to either natural or anthropogenic changes in habitat and resources availability. However, the fact that habitat modification is one of the main factors threatening wild populations of a large number of parrot species (Snyder et al., 2000) suggests that not all species are capable of such behavioral plasticity, or alternatively, that there are threshold levels of habitat modification beyond which parrots cannot respond with behavioral plasticity. Therefore, studies focusing on behavioral plasticity in response to anthropogenic change will help determine when and to what extent such plasticity can occur and improve our understanding of conservation threats and solutions for this highly endangered avian order.

The Yellow-naped Amazon (Amazona auropalliata) is a parrot species that inhabits the tropical dry forest of the Pacific slope from southern Mexico to northern Costa Rica. It is categorized as vulnerable by IUCN, mostly due to habitat loss (IUCN, 2012). Like many parrot species it gathers in large communal night roosts from which it disperses in smaller groups to forage widely during the day. In northern Costa Rica, the tropical dry forest exhibits a seasonal pattern of resource availability and a considerable degree of human-induced habitat modification (Edelman, 1992; Janzen, 1967). There are also marked geographic differences in the spatial distribution of vegetation patches and hence density of resources that result from different land-use strategies (Edelman, 1992). Population genetic studies (Wright et al., 2005; Wright and Wilkinson, 2001) and tracking data (A. Salinas-Melgoza and T.F. Wright, unp. data) suggest that individual Yellow-naped Amazons travel widely across these different land use areas, potentially exposing them to changes in the environment as they move. Hence, individuals might benefit from modifying resource exploitation strategies such as habitat preferences, and roosting and ranging behaviors in different areas. Plasticity in their vocal behavior has been observed when changes in social environment occur (Salinas-Melgoza and Wright, 2012).

The goals of this study were: (a) to evaluate the behavioral strategies for ranging and roosting used by radio-tagged Yellow-naped Amazons to maximize foraging efficiency in the tropical dry forest of northern Costa Rica, and (b) to determine the degree of plasticity in habitat preferences, and the movement and roosting behavior of this parrot species in human-altered landscapes under two land-use regimes. We compared radio-telemetry data of resident birds captured in ranching and farming sites in Guanacaste, Costa Rica to examine the behavioral responses performed by parrots to local conditions. We also looked at the plastic response in the behavior of birds experimentally translocated from the farming to the ranching site.

2. Materials and methods

2.1. Study area

The study was conducted at the southern distributional limit of the Yellow-naped Amazon in the tropical dry forest of the Guanacaste Province of northwestern Costa Rica (Fig. 1). The topography

in the northern region of this Province is slightly hilly with well drained soils (Vásquez-Morera, 1983), which supports predominantly sub-deciduous forest along with premontane moist forest in some areas and a limited gallery forest along water-courses (Hartshorn, 1983). In the southern region of the Province, two landscape units can be distinguished with vegetation differing in structure. The highlands sub-deciduous forest is similar to that found in most of the northern region, while the lowland sub-deciduous forest occurs on the poorly drained soils of the Tempisquito River basin. This lowland sub-deciduous forest is reported to have a combination of a taller, greener dense riparian vegetation combined with swamps in flooded areas (Gordon et al., 1974; Hartshorn, 1983). The rainy season occurs from June to November, and accounts for 85% of the 1656 mm average total annual rainfall for 1980–2009 in Santa Rosa National Park in the northern region (M. M. Chavarria-Díaz, pers. comm.).

Much of the vegetation in this portion of Costa Rica has been altered by human activities, leaving a landscape mosaic of primary forest, human-managed areas, and regenerating patches (Edelman, 1992). The differing economic activities in the northern and southern regions are reflected in region-specific changes in the distribution of the vegetation. The northern region of Guanacaste is dominated by cattle-ranching, with remaining patches of natural vegetation of mainly tropical dry forest in long strips along creeks embedded in an extensive grassland matrix with scattered trees (Hartshorn, 1983; Tosi, 1969). In the southern region, management for intensive agriculture has resulted in clustered remnant patches of dense riparian forest surrounded by large areas of crop fields, a human settlement, and the original highlands sub-deciduous forest. These two regions are located about 30 km apart and separated by urban/industrial areas around the town of Liberia (Fig. 1). The ranching site is composed of two contiguous cattle ranches known

Fig. 1. Location of the two study regions in northern Costa Rica. Small green-rounded dots indicate the ranching region and green-squared dots indicate the farming region. Blue lines indicate streams, large black dots indicate roosts where trapping was performed, and yellow squares indicate towns. Inset indicates location of depicted area in the distribution range of the Yellow-naped Amazon (gray shading). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

as El Guapote and Los Ahogados in the northern region (between 10°52'N85°35'W and 10°42'N85°28'W). Grassland used for pasture occupies 46% of the landscape in this site, while interspersed forest patches occupies almost 54% of the landscape (Fig. A1). The agriculture site corresponds to one farm called El Pelon de la Bajura in the southern region (between 10°30'N85°26'W and 10°26'N85°22'W) (Fig. 1) where cultivated rice and melon fields occupy 55% of landscape, various types of forest comprise about 39% of the landscape, and the remaining 6% is human infrastructure (Fig. A2). Thus these two sites present contrasting landscapes with more dispersed forest in the ranching site, and more concentrated patches in the farming site.

2.2. Trapping and tracking of individuals

Yellow-naped Amazons were captured at large communal roosts at El Guapote, Los Ahogados, and El Pelon de la Bajura (Fig. 1). Nocturnal roosts in this species are traditional gathering sites that can hold up to 300 individuals (Wright, 1996). Birds were trapped during the first 2 h after sunrise and in the 2 h before sunset. Aerial mist-nets were set 5–20 m high in trees adjacent to roost areas to capture birds using playbacks of recordings of local contact calls and duets of mated pairs (Salinas-Melgoza and Wright, 2012).

We captured 42 individuals who were included in this study. Captured individuals were fitted with model SI-2C (Holohil Systems, ON, Canada) or model A3950 (ATS, Isanti, MN) radio-transmitters as neck collars (10 individuals were captured in 2006, nine in 2007, 15 in 2008, and eight individuals in 2009). Both transmitters weighed 2.1% of the average body weight of captured birds (average weight: 519.4 ± 53.3 g, range 400–697 g, $n = 54$, includes some birds captured in a previous study). All captured birds from the Los Ahogados and El Guapote ranching site and those birds captured in 2009 from the El Pelon de la Bajura site were released in the original capture site. During 2007–2008, 15 individuals captured in El Pelon de la Bajura were translocated to the ranching site (seven birds were translocated in 2007, eight individuals were translocated in 2008) to simulate the type of habitat changes an individual might encounter when performing wide ranging movements.

Tracking began immediately after release to monitor the birds' adjustment to the transmitters. Tracking of parrots was performed using omnidirectional and 3-element hand-held Yagi antennas along with TRX-1000 (Wildlife Materials, Carbondale, IL) and TR-5 (Telonics, Mesa, AZ) receivers. Individuals were tracked throughout the field season as described below until the signal was lost, presumably due either to transmitter failure, or birds moving beyond tracking range. The tracking of radio-tagged birds was conducted from May to September in 2006 to 2008, and from January to May in 2009.

Parrots were tracked to determine habitat use and diurnal movement patterns, and nocturnal roost use. Diurnal locations of the Yellow-naped Amazons were obtained during the first 4 h after dawn and 3 h before sunset, when parrots are most active (Salinas-Melgoza and Renton, 2005). When an individual was located, we moved within 50 m to obtain GPS coordinates (Garmin e-trex) and to observe parrot behavior. The location of the individuals was also obtained indirectly through triangulations of two bearings (Nams, 2006). Readings were taken with 3-element hand-held antennas from atop hills and lookouts. Positions were calculated using the software Locate III (Saltz, 1994). In total, only 17% of the locations were obtained through triangulation, which recorded an average error area of 13.2 ± 1.3 ha ($n = 224$). Geographic data was obtained in UTM format and captured in ArcView 3.2 (ESRI, 1996) for analysis. Data obtained on the day of release was not analyzed.

2.3. Estimations of area used

A minimum of 30 locations are recommended to obtain a closer estimation of the home range as an estimation of area used (Seaman et al., 1999). Although the average number of locations we recorded for our individuals was of 63.6 ± 7.7, four out of the seven individuals tracked in 2006 were below the 30 locations threshold limit. Given this limitation, instead of performing evaluations of home ranges we obtained evaluations of activity areas, which are defined as the area in which an individual may be found during a given time period (Thompson et al., 1999). For estimates of activity areas, we included only individuals with a minimum of 20 locations that were recorded at least 20 min apart (established as the minimum time parrots use to cross their activity area, A. Salinas-Melgoza and T.F. Wright, unpublished data), and did not contain the same location recorded consecutively. These criteria allowed us to include the larger number of individuals in the analysis of movement patterns by land use management. Two home-range estimates were used to obtain activity areas to evaluate the influence of resource distribution on space. Both the minimum convex polygon (MCP) (Mohr, 1947) and the kernel were estimated using the Animal Movement (V2.04 beta) (Hooge and Eichenlaub, 1997) and the Home Range Analysis extensions (Rodgers and Carr, 1998) for ArcView. Both estimators were calculated with 95% of all locations for a given individual (95% MCP and 95% kernel), as excluding 5% of the outermost locations removes possibly erroneous outliers from the analysis (Anderson, 1982) and potentially eliminates exploratory movements. In addition to these estimators, we calculated the kernel at 50% to obtain an evaluation of the core areas, which typically represents sites of special biological importance (Coates and Downs, 2005; Samuel et al., 1985). Kernel estimations were performed using a fixed smoothing factor with the least-squares cross-validation (Seaman et al., 1999; Seaman and Powell, 1996). We also estimated core areas for diurnal and roosting locations separately using the 50% kernel to obtain a view of the pattern of roosting and diurnal behavior in each site during the tracking period.

We also evaluated the degree of dispersion of individuals' core areas and their diurnal and roosting social behavior in residents and translocated birds. We performed dyadic comparisons of the degree of overlap in the areas used among resident individuals at each site, and the overlap among translocated individuals as well as that of translocated and resident individuals in the recipient site. We first evaluated the degree of overlap of both the 95% kernel and core areas using all locations to establish if individuals were exploiting the space similarly at each site. We then calculated the overlap in area used among individuals based on independent estimations of diurnal and roosting core areas to compare the diurnal social ranging behavior and roosting behavior at each site.

2.4. Roosting behavior data collection

We determined the number of individuals attending roosts in each site. We recorded the presence of radio-tagged individuals in roost trees, and counted the total number of individuals in the roosting tree attended by focal radio-tagged birds. We performed counts at roosts once per day per roost. All individuals attending the roost arrived before sunset and did not leave the roost in the morning until full light, thus roost size was always estimated during periods of good visibility within 30–45 min before sunset or after sunrise.

2.5. Analysis of habitat preferences

Habitat preferences of parrots were obtained from habitat composition maps of each site (Figs. A1 and A2). These maps were ob-

tained from aerial photographs taken in 1998 from each of the sites in a two-step process. First, a habitat composition map was derived from digitized aerial photos using onscreen cursor in Ilwis 3.7 (Nijmeijer et al., 2001). Second, we ground-truthed the habitat composition maps to obtain a contemporary view of available habitat. The vegetation of 10% random vegetation polygons (Chuvieco, 1995) in the 1998 photographs, the vegetation where all parrot locations were recorded, and images from Google Earth from year 2006 were used in this procedure. Boundaries for each site were set using the outermost locations obtained by tracking individuals in that site. The ranching site map encompassed 32,000 ha, while the farming site map encompassed 4500 ha.

We classified vegetation in the farming region into four habitat types distinguishable in aerial photos. *Infrastructure* included areas of vegetation around small buildings or rural villages. *Dense forest* was dominated by large trees commonly above 23 m (Gordon et al., 1974) and represents remnants of the original vegetation type in the lowlands before intensive land use management. *Deciduous forest* is exclusively found in the highlands and has a canopy height below 23 m (Gordon et al., 1974). *Open field* was located exclusively in the lowlands and was originally dense riparian forest or swamp land subsequently cleared for farming, with a few isolated trees along roadways. The vegetation in the ranching region was classified in four habitat types, two were considered functionally similar to those in the farming region while two others were distinct. Both the *infrastructure* and *deciduous forest* classes were defined in the same manner as in the farming region. The *savannah* category was former deciduous forest that was transformed into grasslands for cattle-ranching, with remnant strips of original vegetation. The *riparian vegetation* category consisted mainly of large trees and associated vegetation exclusively found alongside the larger waterways.

Parrot locations and habitat composition maps were imported into ArcView (ESRI, 1996) for analysis. The proportion of each habitat type used by the parrots was calculated at three levels using the XTools extension in ArcView (Mike, 2003). First we calculated the proportion of each habitat type available in each region. Second, we obtained the proportion of each habitat type within the activity area (95% kernel) of each individual. Third, we obtained the proportion of each habitat type recorded for each location of an individual within the activity area. Proportions of available and used habitat were incorporated in a habitat use analysis using the compositional analysis of Aebischer et al. (1993) as implemented with the compana function from the adehabitat (version 1.8.3) package for R (Calenge, 2006) using 500 randomizations. This approach compares habitat use according to its availability at different hierarchical scales and tests whether habitat use deviates from random. In addition, this analysis provides a ranking of the habitats to identify whether the use of a given habitat differs from expected based on its availability and the relative scale of the ranking. This method allows for between-group comparisons using the within-group between-animal variation at two hierarchical scales: (a) the landscape scale and (b) the activity area scale. The landscape scale indicates how habitat types could influence the location of the activity area in the landscape. The activity area scale indicates how habitats are selected according to availability within the activity area (95% kernel). Habitat types with 0% use were recorded as 0.01%, as recommended by Aebischer et al. (1993).

2.6. Statistical analysis

Data was tested for normality required for parametric analysis with the Shapiro–Wilks test. Most estimations of area used and the roost size measure conformed to normality after log-transformation. Diurnal 95% MCP, 95% kernel, and roosting core area did

not achieve normality. We used ANOVA to test for differences among resident individuals for both sites and translocated individuals for parameters conforming to a normal distribution, and ANOVA on ranks for the remaining parameters (Zar, 1999). A *t*-test was performed to compare roost size between ranching and farming sites. Descriptive statistics are provided as mean ± SE.

3. Results

From the 42 Yellow-naped Amazons radio-tagged in this study, 21 were included in both the analysis of area use and habitat preferences: 7 resident individuals in the farming site (mean number of locations = 70.7 ± 10.3), 7 resident individuals in the ranching site (mean number of locations = 39.3 ± 7.5), and 7 individuals translocated from the farming to the ranching site (mean number of locations = 80.7 ± 16.8) (Table A1). The other 21 individuals were excluded from analysis because they were below the threshold limit on the number of locations. From these individuals, 22.2% were residents from the farming site, while 53% of translocated and 61% of resident birds at the ranching site did not fulfill the requirement to be included in the analysis. From those translocated individuals that were not included in the analysis one took off the transmitter after 4 days of tracking and another individual returned home after 6 days of tracking. We recorded three additional translocated individuals returning to their trapping site after spending 194, 77, and 27 days in the recipient site. However, these individuals were included in the analysis as tracking before return yielded enough locations at the ranching site.
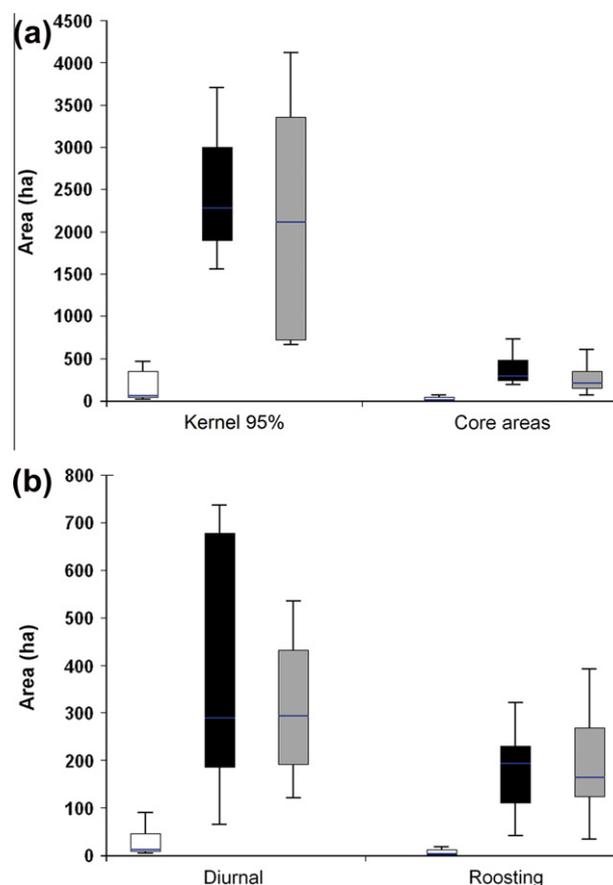
Fig. 2. Kernel 95% and core area size estimations using all locations (a) and core area estimations using diurnal and roosting locations separate (b) by Yellow-naped Amazons in northern Costa Rica. Comparison is shown between farming (white bars), ranching (black bars) regions, and translocated individuals from the farming region (gray bars).

3.1. Estimations of activity area used

Estimates of area used showed significant differences among residents for the ranching and the farming site, and translocated individuals for the 95% MCP ($F_{2,18} = 19.2$, $P < 0.001$), 95% kernel ($H_2 = 13.6$, $P < 0.05$), and core areas ($F_{2,18} = 26.9$, $P < 0.001$). Resident individuals from the farming site used a smaller area than resident and translocated individuals in the ranching site (Fig. 2a). The area used also differed significantly when calculated using only diurnal (95% MCP: $H_2 = 9.6$, $P < 0.01$) and roosting (95% MCP: $F_{2,14} = 8.4$, $P < 0.005$) locations of individuals (Fig. 2b), and was significantly larger in the ranching region for both resident (diurnal 95% MCP: 1041.4 ± 251.5 ha, roosts 95% MCP: 262.2 ± 145.3 ha) and translocated individuals (diurnal 95% MCP: 2169.3 ± 648.5 ha, roosts 95% MCP: 1267.1 ± 472.3 ha) compared to resident individuals in the farming region (diurnal 95% MCP: 156.7 ± 62.0, roosts 95% MCP: 30.7 ± 10.5 ha). Core area estimates also differed significantly between the sites and resident and translocated individuals when using diurnal locations ($F_{2,18} = 18.5$, $P < 0.001$), and roosting locations ($H_2 = 12.6$, $P < 0.01$). Core areas were significantly larger in the ranching region for both resident (diurnal: 394.1 ± 105.6 ha; roosting: 176.5 ± 39.2 ha) and translocated (diurnal locations: 313.3 ± 60.2; roosting: 194.5 ± 49.6 ha)

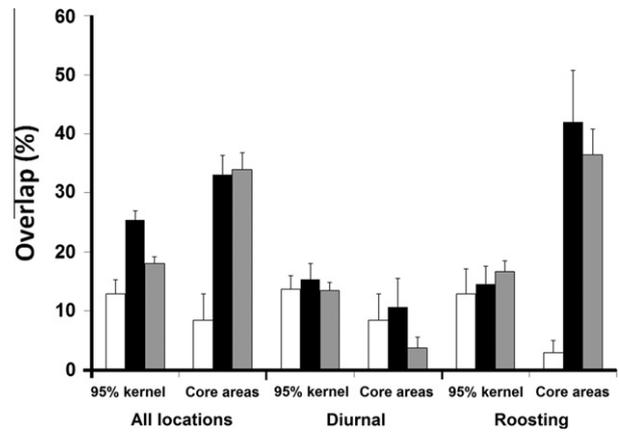**Fig. 3.** Mean (±SE) percent overlap of area used by resident individuals in the farming and ranching sites, and by individuals translocated from the farming to the ranching site. Comparison is shown between farming (white bars), ranching (black bars) regions, and translocated individuals from the farming region (gray bars).

individuals, compared to resident individuals in the farming region (diurnal: 32.0 ± 13.2 ha; roosting: 7.0 ± 2.6 ha; Fig 2b).

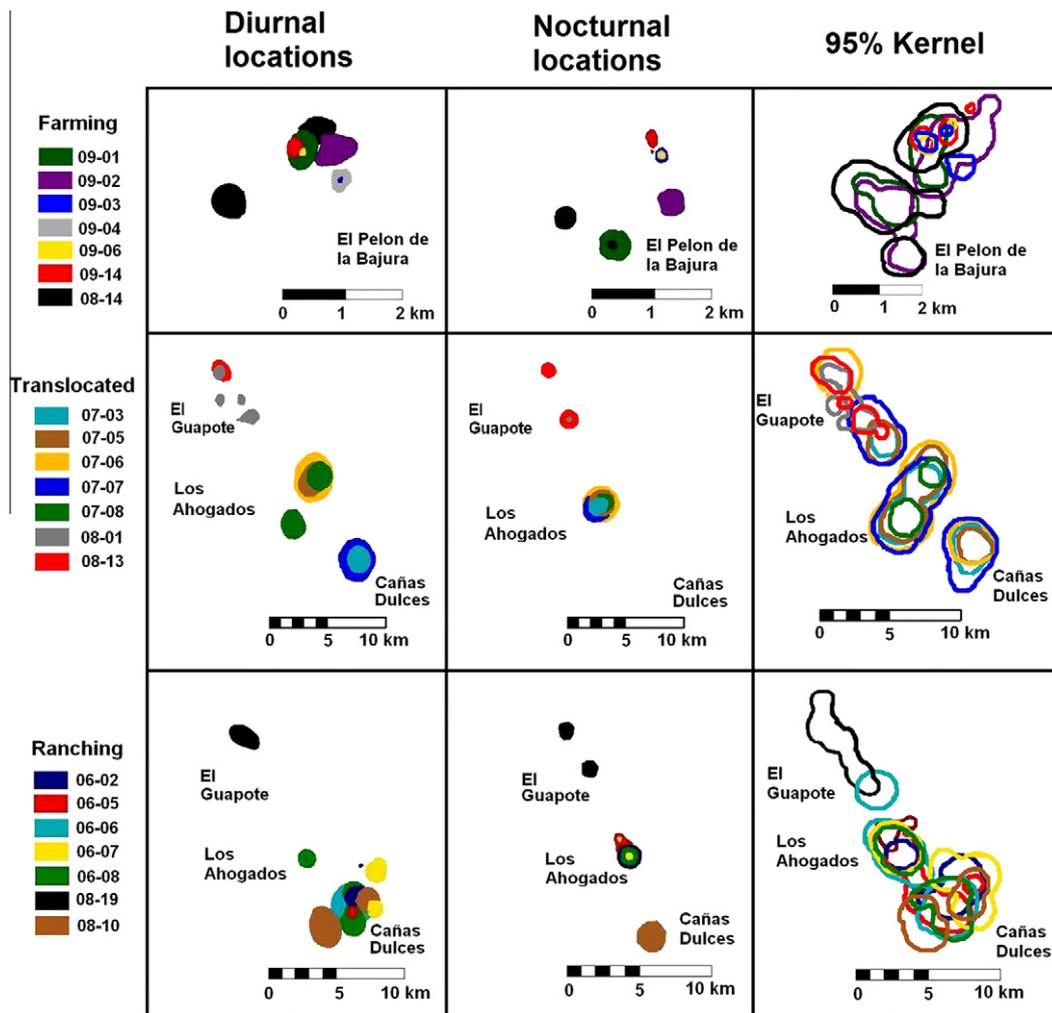**Fig. 4.** Activity area estimates for resident and translocated individuals radio-tracked in the ranching and the farming region. Each color indicates the activity area estimation for one individual from Table A1. Line polygons indicate 95% kernel estimates and filled circles indicates core areas estimates. Habitat types identified at each site are also indicated in map. Note different scales for the two sites.

Table 1
Summary of habitat rankings from the compositional analysis at the landscape scale and the activity area scale for resident and translocated Yellow-naped Amazons in the ranching and farming sites in Guanacaste Province, Costa Rica.

	Preference ranking	Lambda	df	P
Landscape scale				
Residents farming	Dense forest ≫ Infrastructure ≫ Open field > Deciduous	0.0034	3	0.0000
Residents ranching	Infrastructure > Savannah > Riparian ≫ Deciduous	0.0720	3	0.0003
Translocated ranching	Savannah > Riparian > Infrastructure ≫ Deciduous	0.0567	3	0.0001
Activity area scale				
Residents farming	Infrastructure > Dense forest ≫ Open field > Deciduous	0.2936		0.1260
Residents ranching	Savannah > Deciduous > Riparian > Infrastructure	0.2148		0.096
Translocated ranching	Savannah ≫ Deciduous ≫ Riparian ≫ Infrastructure	0.0021		0.0660

≫: Significant differences in relative habitat use between ranked habitats at $P < 0.05$. >: Non-significant differences in habitat use between ranked habitat.

3.2. Activity area overlap

The analysis of the degree of overlap among individuals indicated that residents in the ranching region shared a larger proportion of their area used than residents in the farming region. These differences were found with the 95% kernel and with core area estimators for all locations and roosting core areas separately (Figs. 3 and 4); however, these differences were more marked for core areas. The analysis of overlap between translocated individuals and resident individuals from the ranching region indicated that translocated individuals increased the proportion of shared core areas for all locations and roosting with resident individuals relative to individuals in the farming region from whence they came. This shift in the size of the area used by translocated individuals made their ranging behavior more similar to resident individuals in the recipient site than to individuals in the original trapping site (Fig. 3).

3.3. Regional differences in roosting behavior

We performed roost counts over 52 days: 27 days in the ranching region and 20 days in the farming region. The number of individuals congregating in roosts was significantly larger ($t_{50} = 15.3$, $P < 0.001$) in the ranching region (44.0 ± 3.4 individuals, range = 17–80 individuals, $n = 29$) than in the farming region (4.5 ± 0.7 individuals, range = 1–13 individuals, $n = 23$). The coefficient of variation for counts of individuals at roosts in the ranching region was smaller (42.2%) than that for the farming region (68.9%). A large proportion of radio-tagged individuals in the ranching region habitually used a single roost (Fig. 4); this roost represented 86% of the roosting locations of all individuals in the Los Ahogados site. We identified five different preferred roosting sites used by the seven radio-tagged individuals in the farming region; however, observations indicated additional roosting sites in the region that were not used by these radio-marked individuals. Roosts were dispersed throughout the forested area at this site (Fig. 4). Ninety-three percent of all roosting observations occurred at these five roosting areas. This difference in roosting behavior between the two regions precluded us from using roost counts as an estimation of total parrot numbers in each region.

3.4. Habitat preferences

The ranching and farming regions differed in the habitat types available for parrots. The savannah habitat was found exclusively in the ranching region, while the dense forest habitat was exclusively in the farming region, although in a small proportion. The main habitat type available at the landscape level in the ranching region was savannah, closely followed by deciduous forest (46% and 42% respectively). Open field accounted for most of the area

in the farming region at the landscape level (55%), followed by deciduous forest (27%). Infrastructure was found in a low proportion of the landscape in both regions (ranching: 0.3% and farming: 5.6%).

The results from the compositional analysis indicated that parrots used habitat types non-randomly at the landscape level of analysis regardless of site or residency status (Table 1). In both regions the location of the activity areas within the landscape was significantly driven by vegetation types. The landscape level analysis also indicated that resident and translocated individuals in the ranching region have similar habitat preferences, because although the top three ranking of habitat types varied between resident and translocated individuals, the preferences for these habitats (savannah, riparian and infrastructure) were not significantly different and thus can be considered interchangeable (Table 1). In contrast, the pattern of habitat selection at the level of activity areas did not differ significantly from random; habitats were used according to its availability. The analysis of habitat selection within the activity areas home range indicated that translocated and resident individuals in the ranching region showed the same ranking of habitat types (Table 1). In the farming region, the compositional analysis within the home range indicated similar patterns of land use as at the landscape level due to the interchangeability of habitat types in the ranking position. Here infrastructure and dense forest were found in the top two ranked habitats (Table 1).

4. Discussion

Our study provides insight into the behavioral strategies and degree of plasticity of a threatened parrot species in a human-altered, heterogeneous habitat. Yellow-naped Amazons in both a ranching site, where resources are more dispersed, and in a farming site, where the remaining natural vegetation is concentrated in patches, showed marked contrasts in three behavioral domains of habitat selection, ranging patterns, and roosting behavior that are likely linked to differences in habitat resulting from anthropogenic land use patterns at the two sites. Furthermore, we observed that individuals translocated from the farming to the ranching site adopted the behavioral patterns typical of residents in the ranching site, suggesting significant plasticity in behavioral strategies of individual birds when faced with a landscape with varying degrees of anthropogenic change.

4.1. Ranging and roosting behavior increases with changes with distribution of the resources

Our data on ranging suggest that Yellow-naped Amazons behave in a facultative manner to maximize resource exploitation. We observed that resident individuals from the ranching site used

an area ten times larger in comparison to individuals from the farming site, and that translocated individuals behaved similarly to those resident individuals in the ranching site where they were released. Previous research has shown that the need to fulfill daily requirements in a low resource environment may trigger an increase in movements (Anderson et al., 2005; Anich et al., 2010; Young and Aarde, 2010). Increased activity and movements in periods and areas of potentially low resource availability has been found in other parrot species including the Lilac-crowned Parrot (*Amazona finschi*), the Maroon-fronted Parrot (*Rhynchopsitta terrisi*), and the White-tailed Black Cockatoo (*Calyptorhynchus funereus latirostris*) (Ortíz-Maciel et al., 2010; Salinas-Melgoza, 2003; Saunders, 1980, 1990). These results are consistent with the resource dispersion theory for range size, which states that animals can maximize foraging efficiency by modifying the size of the area used in their daily activities in response to resource density and dispersion (Buchmann et al., 2011; Mitchell and Powell, 2004). This hypothesis suggests that the relative abundance of food affects the size of the area used, with animals maintaining a smaller activity area when there is a higher density of resources (Burt, 1943; McNab, 1963).

We further observed a contrasting pattern of core area use for roosting in each site. Parrots in the ranching region exploited primarily a single roosting area while in the farming region several roosting areas were recorded with a low density of individuals at each roost. These results observed in our study are consistent with the recruitment center hypothesis (Richner and Heeb, 1995, 1996), which suggests that parrots use roosts according to the differing distribution of resources imposed by the land-use strategies, thereby increasing the benefits obtained from social foraging and efficiency in resource exploitation. When resources are dispersed, as in the ranching site, roosting is predicted to increase as a mechanism to enhance recruitment of fellow foragers. Conversely, when resources are more spatially concentrated, as in the farming site, roosting should decline as the benefits of social foraging by recruitment at this congregation site decreases. Alternative explanations to these differences in roosting behavior include differential predation levels at the two sites (Beauchamp, 1999), or differences in the age structure of the two populations coupled with age-related differences in roosting strategies (Blanco and Tella, 1999). While we did not collect data either on predation risk nor the age structure of these two populations we have no reason to suspect that either differs as strongly between these two populations as does resource dispersion.

4.2. Pattern of habitat selection driven by vegetation

Yellow-naped Amazons showed significant habitat preferences at the landscape level and to a lesser extent habitat preference within the activity areas. These habitat preferences differed between the two sites, reflecting the fact that available habitat types differed between sites and may in turn drive the behavioral differences observed for parrots. Savannah is the predominant habitat type in the ranching region and was found in the top ranked habitats used by both resident and translocated birds at the landscape and activity area levels. It is unclear whether this preference represents an adaptive strategy for the birds. Preference for the savannah does not necessarily mean it is the best habitat type for the Yellow-naped Amazon, but rather it could indicate the ability of the species to adapt to this modified habitat. Food resources in savannah may be at a lower density in this ubiquitous habitat type due to the low density of trees where parrots forage; hence, individuals may be aiming to compensate for this scarcity by increasing the area covered to fulfill daily energetic requirements. Alternatively, this habitat preference could represent an ecological trap (Battin, 2004) arising due to the predominance of savannah.

In contrast, habitat preferences in the farming region at the landscape and activity area levels were driven primarily by the distribution of dense forest and infrastructure, as these two preferred habitat types are highly clumped and adjacent to each other. Food resources could be concentrated in the dense forest and the infrastructure habitat types, allowing individuals to perform shorter moments in the farming region. Habitats regularly showing a higher availability of food resources are preferred by parrots in both natural (Renton, 2001; Salinas-Melgoza, 2003) and anthropogenic habitats (Strubbe and Matthysen, 2010).

4.3. Flexibility in ranging and roosting behavior

Yellow-naped Amazons showed plasticity in their habitat selection, roosting and ranging behavior when experimentally moved from one site to another. Habitats with contrasting food resources availability have been found to influence the pattern of movements in a number of mammal (Herfindal et al., 2005; López-Bao et al., 2009; Saïd et al., 2009) and bird species (Anich et al., 2010; Roth and Vetter, 2008; Siffczyk et al., 2003; Wiktander et al., 2001). In addition, experimental manipulation of resource density in both Dark-eyed Juncos (*Junco hyemalis*) and Iberian Lynx (*Lynx pardinus*) (López-Bao et al., 2009; Roth and Vetter, 2008) also demonstrate that individuals may adjust the magnitude of their movements in a manner consistent with the resource dispersion hypothesis. Our results showing that translocated individuals from the farming region matched the pattern of habitat selection, and the ranging and roosting behavior of resident individuals in the ranching region indicate that the Yellow-naped Amazon also alters its behavior when moved into unfamiliar areas with different resource distributions. Previous work in the Yellow-naped Amazon has shown that translocated birds will show behavioral plasticity in the vocalizations they produce (Salinas-Melgoza and Wright, 2012); this study extends the behavioral domains in which such plasticity is observed.

One plausible explanation to this behavioral plasticity is that the social behavior of this species enabled translocated individuals to follow resident individuals at the new site. Social cues from resident individuals may have caused translocated birds to modify their habitat preferences, increase the magnitude of the movements, and join local roosts. This behavioral flexibility based on social information may be advantageous for a species that performs wide-ranging movements, especially when familiar habitat is not available in a new area. It may also play a role in the success of those invasive species with high degrees of sociality (Wright et al., 2010). An alternative explanation for this plastic behavior is that individuals from the farming site have visited the ranching site at some point during dispersal or ranging and that prior experience with the ranching site allowed translocated individuals to quickly adapt to differences they encountered there. There is evidence suggesting that Yellow-naped Amazons would be able to travel between these two sites in as short time as 6 days (A. Salinas-Melgoza and T.F. Wright, unp. data). This relatively short time to return to the original trapping site would suggest that some translocated individuals were familiar with the route connecting the sites. On the other hand, our radiotracking of resident individuals never showed any instances of birds moving between sites, suggesting that inter-site movements by established birds are rare.

Our results from translocated individuals could also reflect exploratory movements in the new area. Most translocated individuals were recorded using exclusively the roost where they were released and showed a high fidelity to foraging areas used by resident birds in the ranching region. However, we did record translocated individuals making occasional long-range movements (>10 km) away from these areas over the monitoring period. We do not know to what extent these long-range movements reflect

exploratory movements by translocated individuals, efforts to compensate for differences in habitat between the source and the recipient site, or imperfect copying of space use patterns of resident individuals. However, the use of roosts established by resident individuals and the distribution of diurnal core areas suggest translocated parrots generally are copying the movements of residents. Evaluations of the ranging and roosting behavior of individuals reciprocally translocated from the ranching to the farming site could help to disentangle the combined effect of exploratory movements with a response to the density of resources.

Our results also suggest some individual variation in plastic capabilities. Such plasticity has been seen in responses of other species to human-altered landscapes (Carrete and Tella, 2011). In the case of the Yellow-naped Amazon, we saw variation in whether translocated birds returned home to their capture site or remained in the new site. These differences may be associated with age classes as the translocated individual that we recorded staying the longest in the recipient area (over 1 year) was a juvenile.

4.4. Caveats

Resource availability and distribution were not directly measured in the present study due to the large scale over which parrots were moving. Despite this limitation, we think our assumption that land use regimes result in different distributions of resources in ranching versus farming areas is well-founded. The scale of studies on the ecological determinants of space use often limit the direct evaluation of resource availability and indirect approaches are commonly used (Anderson et al., 2005; Dussault et al., 2005; Ferguson et al., 1999; Young and Aarde, 2010). In our case, estimations of resources availability for the Yellow-naped Amazon can be approximated by the pattern of forest cover because parrot diet is mainly composed of seeds and flowers from trees, and in this population has never been observed to forage on the ground (A. Salinas-Melgoza and T.F. Wright, unp. data). An additional limitation to our study is that individuals at different sites were monitored at different times; we believe, however, based on unpublished observations (A. Salinas-Melgoza and T. Wright) that our results represent responses to spatial rather than temporal variation.

4.5. Implications for conservation

Many parrot species, including the Yellow-naped Amazon, are threatened due to a combination of habitat loss and capture for the pet trade (Snyder et al., 2000; Wright et al., 2001). Translocation programs are often considered as a means of increasing the size of threatened populations or reestablishing extirpated populations within historical ranges (IUCN, 1998), frequently used as conservation strategies for wildlife (Griffith et al., 1989) and conservation of parrots (Brightsmith et al., 2005; Sanz and Grajal, 1998; Snyder et al., 2000; White et al., 2005, 2012). A prime example is the attempts to reintroduce the Thick-billed Parrot (*Rhynchopsitta pachyrhyncha*) to its former distribution range, the failure of which was attributed in part to the lack of plasticity of the captive-raised released individuals (Snyder et al., 1994). Our data from translocated Yellow-naped Amazons suggest that translocations of wild birds may be a more viable strategy, particularly when resident individuals are available to provide translocated individuals with models of appropriate local foraging strategies. Such models were not available in the case of the Thick-billed Parrot.

This study provides quantitative information on the plastic response of the Yellow-naped Amazon that could be used to predict behavioral responses in translocation attempts in other parrots. It has been suggested that release attempts are best performed in areas with similar habitats and selection pressures to which translocated individuals are adapted (Bradley et al., 2012; Sarrazin and Legendre, 2000). However in practice, adequate release sites may be limited and individuals may frequently be released in areas where habitat features differ from those of the source area (Lloyd and Powlesland, 1994). Hence the scenario to which our translocated individuals were exposed may be common not only for the Yellow-naped Amazon but also for other parrots should reintroductions and translocations become more common. In addition, the pattern of philopatry found in this study suggests that interindividual variation in plasticity could be one of the factors influencing the success of translocation attempts. This plasticity pattern could account for the large number of translocated individuals normally required in translocation efforts to assure that some of them will stay (Armstrong and Seddon, 2007; Fischer and Lindenmayer, 2000). A growing number of conservation-oriented parrot translocations appear to have been successful (White et al., 2012; James Gilardi, pers. comm.). Although data for many of these translocations are not published, informal reports of persisting populations suggests that behavioral plasticity in individuals experiencing new environments may be more widespread than previously considered.

5. Conclusions

Our results illustrate that one parrot species can alter its movement and spatial and habitat use patterns to adapt to human induced changes in habitats. Such adaptive behavioral plasticity represents an important response to human-induced changes in habitats. Although our results point to a short-term adaptive response to changes in habitat at regional scales due to land-use strategy, such plasticity could also be adaptive when facing long-term changes such as human-induced global change. Further work examining the types and limits of such plasticity will further our understanding of how animal species will respond to global climate change and habitat alteration. Reciprocal translocations between sites differing in vegetation conditions would be a key component in future research in this species to disentangle potential masking factors in the plastic response.

Appendix A. Appendix

See Table A1.

Table A1
Activity area estimates in hectares for Yellow-naped Amazons radio-tracked in northern Costa Rica from 2006 to 2009.

ID #	Capture site	Treatment	Land use at release site	Locations	Tracking days	95% kernel	95% MCP	Core area	Tracking period
06-02	Aho	R	Ranching	57	50	1775.0	1469.2	185.8	09 June 06–28 July 06
06-05	Aho	R	Ranching	29	23	2456.8	473.2	414.4	06 July 06–28 July 06
06-06	Aho	R	Ranching	25	23	3839.0	1839.8	786.7	07 July 06–29 July 06
06-07	Aho	R	Ranching	32	22	3184.5	1415.7	506.1	08 July 06–29 July 06
06-08	Aho	R	Ranching	28	20	2283.6	555.0	294.0	10 July 06–29 July 06
08-10	Aho	R	Ranching	27	45	2256.3	2875.1	288.6	24 June 08–5 Aug 08
08-19	Gua	R	Ranching	77	75	1504.3	1560.9	225.3	23 May 08–5 Aug 08
09-01	P B	R	Farming	42	56	216.3	156.9	23.7	19 March 09–13 May 09
09-02	P B	R	Farming	93	49	397.8	439.7	50.4	21 March 09–11 May 09
09-03	P B	R	Farming	72	51	57.3	53.4	6.3	24 March 09–13 May 09
09-04	P B	R	Farming	77	51	57.4	60.0	7.1	24 March 09–13 May 09
09-06	P B	R	Farming	105	53	12.7	41.8	2.9	21 March 09–13 May 09
09-14	P B	R	Farming	78	37	40.7	41.8	5.0	08 April 09–14 May 09
08-14	P B	R	Farming	28	27	477.6	219.8	66.3	22 March 08–17 April 09
07-03	P B	T	Ranching	137	78	2117.0	3814.5	205.2	11 July 07–27 Sept 07
07-05	P B	T	Ranching	102	76	2298.0	4919.8	208.7	13 July 07–27 Sept 07
07-06	P B	T	Ranching	49	67	3712.8	4454.3	396.4	21 July 07–26 Sept 07
07-07	P B	T	Ranching	79	64	4224.0	3442.5	655.0	21 July 07–23 Sept 07
07-08	P B	T	Ranching	33	59	652.2	1421.4	142.0	26 July 07–23 Sept 07
08-01	P B	T	Ranching	132	115	701.1	722.3	44.4	8 May 08–28 July 08
08-13	P B	T	Ranching	33	56	783.7	192.9	170.7	1 June 08–27 July 08

Aho = Los Ahogados, Gua = El Guapote, PB = El Pelon de la Bajura, R = resident, T = translocate.

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2012.12.013. These data include Google maps of the most important areas described in this article.

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