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PERENNIAL PAIR BONDS IN AN ACCIPITER: A BEHAVIORAL RESPONSE TO AN URBANIZED LANDSCAPE?

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ABSTRACT.—In some urban environments, human activities enhance resources for avian species, providing habitat that can support year-round occupancy. If both members of a mated pair stay on their breeding territories year-round, close proximity of pair members throughout the year may increase the potential for interactions outside the breeding season. Under these circumstances, avian species that would otherwise terminate their bonds following the breeding season may form perennial pair bonds. We examined behavior of mated pairs of adult Cooper's Hawks (*Accipiter cooperii*) during the nonbreeding season in an urban environment to determine whether pairs retained their breeding territories outside the breeding season and if year-round maintenance of territories influenced the duration of pair bonds. Home ranges and core areas of pair members largely overlapped. Pair members remained close to the nest site they used during the previous breeding season, avoided neighboring conspecifics of the same sex, and selected areas within their home ranges that supported abundant avian prey and contained vertical vegetation structure. Pair members interacted throughout the nonbreeding season via acts of courtship and vocalizations, mainly in areas near the nest site. Perennial pair bonds in Cooper's Hawks in this urban environment are likely a response to high availability of prey throughout the year and facilitated largely by fidelity to and retention of all-purpose territories year-round. For Cooper's Hawks in this urban environment, maintaining pair bonds continuously may confer several advantages such as early initiation of breeding and higher reproductive success.

KEY WORDS: *Cooper's Hawk*; Accipiter cooperii; *Accipiter*; *habitat selection*; *pair bonds*; *social behavior*; *space use*; *urban*.

PAREJAS PERENNES EN UN ACCIPÍTRIDO: RESPUESTA COMPORTAMENTAL A UN AMBIENTE URBANIZADO

RESUMEN.—En algunos ambientes urbanos, las actividades humanas aumentan los recursos para las especies de aves, proporcionando un hábitat que puede mantenerse ocupado durante todo el año. Si ambos miembros de una pareja se quedan en sus territorios de cría a lo largo de todo el año, la cercanía de los miembros de la pareja a lo largo del año puede incrementar el potencial de interacciones fuera de la época reproductiva. Bajo estas circunstancias, las especies de aves que de otra manera finalizarían sus lazos tras la época reproductora, pueden formar parejas perennes. Examinamos el comportamiento de parejas de adultos de *Accipiter cooperii* durante la época no reproductora en un ambiente urbano para determinar si las parejas retienen sus territorios de cría una vez finalizada la época reproductora y si el mantenimiento de los territorios a lo largo del año influyó en la duración de los lazos de pareja. Las áreas de campeo y las áreas núcleo de los miembros de la pareja se solaparon en gran medida. Los miembros de la pareja permanecieron cerca del lugar de nidificación que utilizaron durante la época reproductora anterior, evitaron a vecinos conespecíficos del mismo sexo y seleccionaron áreas dentro de sus áreas de campeo que mantuvieron una abundante cantidad de aves-presa y que presentaron una estructura vegetal vertical. Los miembros de la pareja interactuaron a lo largo de la época no reproductiva a través de actos de cortejo y vocalizaciones, principalmente en áreas cercanas al nido. Probablemente, las parejas perennes en *A. cooperii* en este ambiente urbano son una respuesta a la elevada disponibilidad de presas facilitada ampliamente por la fidelidad y la retención de los territorios para cualquier propósito, a lo largo del año. Para las parejas de *A. cooperii* en este ambiente urbano, mantener los lazos de pareja

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continuamente puede conferir numerosas ventajas tales como un inicio temprano de la reproducción y un mayor éxito reproductivo.

[Traducción del equipo editorial]

In birds that are socially monogamous, the duration of pair bonds can range widely from ephemeral to perennial (Lack 1968, Rowley 1983, Fowler 1995, Black 1996). For many species, interactions between members of a mated pair can be characterized by two distinct seasons, the breeding and the nonbreeding. Ephemeral pair bonds are formed and last only during the breeding season (Black 1996). After breeding activities cease, interactions between pair members subside and pair bonds dissolve. Thus, for species with ephemeral pair bonds, the division of the breeding and nonbreeding season is well delineated from a behavioral perspective. In contrast, the distinction between the breeding and nonbreeding season is blurred in species that have perennial pair bonds because interactions between pair members persist throughout the annual cycle (Black 1996).

The costs and benefits of different types of pair bonds depend largely on life-history strategies of the species, population demography, and reproductive tradeoffs (Choudhury 1995, Black 1996). Ecological constraints also play an important role in duration of pair bonds and mate fidelity, and various types of pair bonds can enhance fitness under different environmental conditions (Rowley 1983, Black 1996). There may be little incentive, for example, for species that are migratory and short-lived to uphold perennial pair bonds because of the high energetic costs of maintaining contact with a mate through migration, and the uncertainty of whether a mate will survive to the subsequent breeding season. The benefits of maintaining perennial pair bonds, however, may outweigh the costs for species that are nonmigratory, long-lived, and inhabit environments that allow them to use an all-purpose territory year-round (Rowley 1983, Ens et al. 1996, Black 1996, Cézilly et al. 2000).

Among predatory birds, perennial pair bonds may occur in species that occupy the same territory throughout the year (Cade 1955, Thorstrom et al. 2001, Delgado and Penteriani 2007). Moreover, in predatory birds, site fidelity may be closely linked with mate fidelity and the decision to stay with or leave a mate may be intertwined with the decision to stay in or abandon a territory, and be dependent on several factors, including reproductive success, age, and quality of territory (Newton and Marquiss 1982, Forero et al. 1999, Thorstrom et al. 2001, Linkhart and Reynolds 2007, Bai and Severinghaus 2012). In environments where resource levels change seasonally or territory quality is low, pair members may leave their territories in search of sufficient food supplies and higher quality territories, thus decreasing the likelihood of perennial pair bonds and mate fidelity (Newton and Marquiss 1982). If local resource conditions are consistent seasonally and territory quality is high, individuals can maintain all-purpose territories year-round and this may prolong the longevity of pair bonds throughout the year and promote mate fidelity (Newton 1979). Therefore, the costs and benefits and ability to maintain perennial pair bonds may shift across environmental gradients.

Urban areas can provide high quality habitat for some avian species because of human-mediated changes in ecological processes, such as reduced predation, reduced variability in microclimate, and increased availability of resources (Marzluff et al. 2001, Shochat et al. 2006). Species able to colonize urban environments, and take advantage of high quality habitats, may exhibit behaviors and demographic performances that differ from their nonurban counterparts, if they have some behavioral plasticity (Shochat et al. 2006, Møller 2010, Sih et al. 2011). Exploitation of the resources and ecological conditions in urban areas could result, for example, in higher rates of survival, reproduction, site fidelity, and changes in breeding phenology (Yeh and Price 2004, Møller 2010, Stracey and Robinson 2012, Martin et al. 2014).

Urban populations of Cooper's Hawks (*Accipiter cooperii*) are becoming increasingly common throughout the United States (Rosenfield and Bielefeldt 1996, Boal and Mannan 1998, Roth et al. 2008, Stout and Rosenfield 2010), and often exhibit marked ecological and demographic differences relative to Cooper's Hawks inhabiting nonurban environments (Rosenfield et al. 1996, Boal and Mannan 1999, Mannan and Boal 2000, Mannan et al. 2008, Roth et al. 2008, Stout and Rosenfield 2010, Boggie and Mannan 2014). Cooper's Hawks are thought to have ephemeral pair bonds, with pair members becoming solitary during the nonbreeding season (Snyder and Snyder 1991, Rosenfield and Bielefeldt 1993). In nonurban environments in Florida, for example, following the breeding season, female Cooper's Hawks

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frequently desert their breeding territories and mates, whereas males retain their breeding territory year-round (Millsap et al. 2013). The breeding dispersal of female Cooper's Hawks in Florida is likely a response to low prey availability and corresponding low provisioning rates during the breeding season (Millsap et al. 2013). In urban areas in southeastern Arizona, however, Cooper's Hawks are year-round residents, and exhibit high rates of provisioning at nests, and site and mate fidelity (Boal 2001, Estes and Mannan 2003, Mannan et al. 2007). Areas rich in resources that support year-round residency in both male and female Cooper's Hawks also may increase the potential for departures from the typical ephemeral pair bonds in this species, in that close proximity throughout the year may facilitate interactions between pair members outside the breeding season.

Our objectives were to determine if an urban environment could influence the social dynamics between pair members of Cooper's Hawks during the nonbreeding season. We quantified space use of males and females to determine whether there was a large degree of spatial association in home ranges and core areas of pair members and whether pair members remained near their nest sites and breeding territories. We also examined habitat selection within home ranges of mated males and females to identify factors that influenced use of the urban environment and to determine whether pair members selected similar habitat within their home ranges during the nonbreeding season. Finally, we documented behaviors to determine whether pair members interacted and maintained pair bonds.

METHODS

Study Area. We studied social behavior of mated pairs of Cooper's Hawks during the nonbreeding season in the greater metropolitan area of Tucson, Arizona (32°N, 111°W), an area encompassing ca. 1600 km^2, with a mean elevation of 730 masl, and an estimated human population of approximately 982,000 residents (United States Census Bureau 2010). Tucson is located in the Sonoran Desert and is characterized by Lower and Upper Sonoran vegetation (Brown et al. 1979). Much of the native vegetation in Tucson, however, has been replaced with nonnative plant species, including large trees (Aleppo pine [*Pinus halepensis*], Afghanistan pine [*P. eldarica*], *Eucalyptus* spp.) that are used commonly by predatory birds. Each spring the greater area of Tucson is intensely surveyed for new and established active nests to account for all breeding pairs of Cooper's Hawks, and currently over 200 are monitored annually as part of a long-term study (Mannan et al. 2008). From this sample of nests, we selected a cluster of 15 within an area of 1100 ha and made a special effort to find any new nests that were within this area. The area contained a mix of commercial districts, high-to-low density residential developments, relatively undeveloped areas (e.g., parks, golf courses), and natural and disturbed open spaces and washes.

Hawk Capture and Radiotelemetry. We used balchatri or dho-gaza traps (Berger and Mueller 1959, Bloom 1987) to capture mated pairs of Cooper's Hawks. We captured and radio-tagged male hawks from March to early-June, with the majority of hawks captured before May. We captured and radio-tagged females after their nestlings hatched in mid-May. We used a modified synsacrum harness (Rappole and Tipton 1991, Roth et al. 2008) composed of 0.64-cm-wide Telfon® ribbon (Telonics, Mesa, Arizona, U.S.A.), with an integrated cotton suture (i.e., a weak link), to attach radio transmitters (RI-2C, 6 g, 12 mo, Holohil Systems Ltd., Carp, Ontario, Canada) to hawks. Combined mass of the transmitter and harness was ≤2.5% of the body mass of individual hawks.

We radio-tagged 10 pairs of hawks at the beginning of the breeding season in 2010. We recorded locations of male hawks for up to 12 consecutive months from mid-March through mid-February and locations of female hawks for up to nine consecutive months from early-June through mid-February. We defined the nonbreeding season as the period between dispersal of the young out of their natal area (ca. 11–13 wk after hatching; Mannan et al. 2004) and initiation of nest building the following year. Timing of the dispersal of the fledglings and initiation of breeding varied among pairs, but generally occurred in August and February, respectively. We lost radio contact with one pair 1 wk after capture, and another pair in late-September after collecting only 15 locations; we excluded both of these pairs from analyses. Three males and one female either perished or the battery in their transmitter died near the end of the nonbreeding season, but we had located each of these hawks 26, 27, 30, 23 times, respectively, throughout the nonbreeding season. We generated area observation curves (Odum and Kuenzler 1955) for these hawks and the sizes of their home ranges stabilized before the last locations were collected; data for all three

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hawks were used in analyses. We located each of the other hawks ≥40 times.

We used an omni-directional antenna to locate the general area of hawks and then used a 2-element handheld yagi antenna to home in to their exact location (Kenward 2001). We confirmed the location of each hawk visually when possible. If we could not see a hawk, we used triangulation (Kenward 2001) to estimate its location. Percent of locations that were confirmed visually throughout the nonbreeding season was 93.9% (n = 709). After a hawk was located, we recorded its behavior, a detailed description of location, and date and time. We defined mate interactions as vocalizations between males and females (e.g., female "mewing" or "kekking," male kekking without prey), acts of courtship (e.g., prey delivery from male to a female, male with prey kekking for female who is perched nearby) and instances when males and females were feeding or perched within 110 m of each other when time between their locations was ≤30 min. We used ArcGIS ArcMap 10.1 (ESRI, Redlands, California, U.S.A.) to geocode locations to multispectral orthophoto imagery of Pima County, Arizona, with a 10-cm spatial resolution (Pima County Association of Governments 2009). We stored the locational attributes in a geodatabase. High-resolution imagery allowed for accurate placement of locations. We recorded locational and observational data at least three times per week for each hawk and alternated uniformly the time of day we located a hawk (morning, midday, and afternoon/evening periods) from the day after the hawk was radio-tagged to when the subsequent breeding season began approximately 1 yr later. At the beginning of the subsequent breeding season, we located each hawk only once per week because they had either returned to their previous nest site, moved to a new nest site, or the hawk had died, or the transmitter had failed and could not be located. We tried to locate both members of a pair on the same day as close in time as possible, and as frequently as possible, to assess distances between mates and record mate interactions. When pair members were located on the same day, the time between locations of pair members never exceeded 1 hr. We avoided issues of spatial autocorrelation by allowing sufficient time to elapse between an individual's locations (≥12 h), so a hawk had time to move from one end of its home range to the other (White and Garrott 1990). We acquired 698 (for males n = 341, for females n = 357) telemetry locations during the nonbreeding season. All birds were captured and banded under Federal Bird Banding Permit 21794 and Arizona Scientific Collecting Permits SP594750 and SP693796. All field methods followed protocols approved by the Institutional Animal Care and Use Committee (Protocol Number 08-144).

Home Range and Overlap Estimation. We used Animal Space Use 1.3 Beta (Horne and Garton 2009), Geospatial Modeling Environment 0.5.3 Beta (Beyer 2012), and ArcGIS version 10.1 (ESRI, Redlands, California, U.S.A.) to estimate size of home ranges and core areas. We used the 95% adaptive kernel method and the 50% adaptive kernel method to estimate home ranges and core areas, respectively, for both males and females. We used the likelihood-cross validation (CVh) smoothing parameter for each adaptive-kernel estimate because the method is less biased and less variable than other frequently used smoothing parameters, such as least-squares cross validation (Horne and Garton 2006).

To assess spatial association of pair members, we examined if distance between mates was different from random throughout the nonbreeding season. For each mated pair, we measured distances between observed locations within the home range of a pair member and observed locations of its mate, then compared these to distances between random locations within the home range of a pair member and observed locations of its mate. We also estimated overlap of home ranges of pair members by calculating the area of overlap between home ranges of pair members and dividing it by the area of the home range for each member. We used the same procedure to calculate overlap between core areas of pair members. For each hawk we also calculated the proportion of overlap of its home range with home ranges of neighboring conspecific males and females by summing all overlap for neighboring conspecifics of each sex and dividing by the area of the home range. We used the same procedure to calculate overlap of core areas of neighboring conspecifics.

Habitat Selection. We estimated habitat availability for each hawk by drawing a random sample of points within their home range equal to the number of telemetry locations within their home range, with telemetry locations representing resource units used (design III; Manly et al. 2002). We assessed habitat selection by comparing resource conditions at used locations to resources conditions at random locations within home ranges of pair members (third-order selection; Johnson 1980).

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We identified habitat features that we thought would influence habitat selection of pair members. We used an urban land-use classification system called Wildlife Habitat Inventory Project (WHIPS) that offered land-use mapping of higher resolution than GAP mapping analysis to characterize land use within home ranges (Shaw et al. 1996). We used land-use types in the aerial imagery to update land-use types in the WHIPS mapping that were incorrectly classified or had changed. Types estimated were: low-density residential (1–6 residences per 0.4 ha [RHA]), high-density residential (>6 RHA), open space (natural open spaces with remnant vegetation, graded vacant land), commercial property (industrial, public buildings, schools), recreation (golf courses and associated recreation areas and neighborhood parks <4 ha, agricultural lands, roadways, and washes (channelized disturbed washes with little vegetation, undisturbed washes with bank-stabilizing vegetation, and riparian areas).

In Tucson, Cooper's Hawks build nests in groves of large nonnative trees and concentrate their activities at the nest site during the breeding season (Boal and Mannan 1999, Boggie and Mannan 2014). Competition for these groves of large nonnative trees is likely high, so for each individual we measured the distance to its nest from each telemetry location and from each random location to determine if hawks remained near their nest site during the nonbreeding season. We also measured proximity to the nearest core area of neighboring hawks from each telemetry location and each random location to determine if proximity to neighboring conspecific hawks (both male and female) influenced habitat selection.

We selected five covariates and interactions between these covariates to develop a set of *a priori* candidate models to explain variation in habitat selection within home ranges of pair members and present only models that we thought were the most biologically plausible (Table 1). We did not include distance between mates as a covariate in the models because we were unable to relocate pair members on the same date for each sampling occasion; thus, we did not have estimates of distance between mates for every observation. We included a random-intercept-only model that represented our null model (model 1). We hypothesized that in our study area, male and female hawks would avoid open spaces and land-use types that lacked vegetation structure and select land-use types that are positively correlated with prey densities, such as residential areas (model 2), and allowed this to vary by sex (model 3; Boal 1997, Germaine et al. 1998, Mannan and Boal 2000). We also considered that if pair members maintained their breeding territories during the nonbreeding season, pair members would remain near their previous year's nest site and distance to nest would influence habitat selection (model 4). We hypothesized that because males of many predatory birds are the primary territory holders, males would likely stay closer to the nests than females (model 5). Furthermore, we considered that both distance to nest and land-use type may additively influence habitat selection (model 6), and that selection of land-use types may or may not differ between pair members, but the effect of distance to nest would depend on sex (model 7, model 8). In addition to models that accounted for the influence of distance to nest and land-use type, we specified several models that incorporated the effect of proximity to nearest core area of neighboring conspecifics to assess how territoriality influences habitat selection. We hypothesized hawks would avoid the nearest core areas of neighboring conspecifics and considered all of the covariates in model 7, but included proximity to nearest core area of neighboring conspecific as an additive effect (model 9), and allowed this to vary by sex (model 10). Finally, we hypothesized that the influence of proximity to the nearest core areas of neighboring conspecifics would likely depend on the sex of the hawk occupying the neighboring core area and also the sex of the hawk selecting an area (model 11).

Statistical Analyses. We used paired *t*-tests to compare sizes of home ranges and core areas between pair members, overlap of home ranges and core areas of pair members, and to determine whether observed distances between mates were different than random. We used the locally weighted regression (LOESS) function in R (R Development Core Team 2012) to fit smooth lines to and model the relationship between distance between mates and month of the nonbreeding season, and distance to nest and month of the nonbreeding season. When necessary, we log-transformed data when underlying distributions did not meet assumptions of homogeneity of variance and normality.

We used a generalized linear mixed-effects model to estimate a population-level resource selection function to predict relative probability of use (Manly et al. 2002). We used the glmer function from the lme4 package (Bates and Bolker 2012) in R (R Development Core Team 2012) for the analysis. We

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Table 1. Results of model selection for models predicting habitat selection within home ranges of mated adult male and female Cooper's Hawks during the nonbreeding season in Tucson, Arizona, 2010–2011.

MODEL NO.	MODEL[1]	K[2]	$\Delta AICc$[3,4]	w_i[5]
11	SEX + NSEX + NEST + NCA + LAND + (SEX × NEST) + (SEX × NCA) + (NSEX × NCA) + (SEX × NSEX) + (SEX × NSEX × NCA)	19	0.00	1.00
10	SEX + NEST + NCA + LAND + (SEX × NEST) + (SEX × NCA)	15	46.36	0.00
9	SEX + NEST + NCA + LAND + (SEX × NEST)	14	58.46	0.00
7	SEX + NEST + LAND + (SEX × NEST)	13	78.03	0.00
8	SEX + NEST + LAND + (SEX × NEST) + (SEX × LAND)	20	85.04	0.00
6	NEST + LAND	11	103.33	0.00
2	LAND	10	153.51	0.00
3	SEX + LAND + (SEX × LAND)	18	159.07	0.00
5	SEX + NEST + (SEX × NEST)	6	197.42	0.00
4	NEST	4	223.12	0.00
1	INTERCEPT ONLY	3	295.74	0.00

[1] SEX = sex of hawk, reference level "female"; NEST = distance to individual's nest within home range; LAND = land-use type with eight levels, reference level "low-density residential"; NCA = proximity to nearest core area of neighboring hawks; NSEX = sex of hawk occupying nearest neighboring core area, reference level "female"; INTERCEPT ONLY = random intercepts only model for benchmark comparison.

[2] K = number of parameters in model.

[3] Akaike's Information Criterion adjusted for small sample size (AICc) value for top model (model 11) was 1645.54.

[4] Difference between AICc top model and other model.

[5] Relative Akaike weight of each model.

classified individual hawks nested within their mated pair as random intercept effects in the model to account for uneven sample sizes and variation in selection or available resources among pairs and individuals (Gillies et al. 2006). We used the MCMCglmm package (Hadfield 2010) in R (R Development Core Team 2012) to generate 10,000 Markov Chain Monte Carlo (MCMC) samples and 95% Highest Posterior Density intervals (HPD intervals) to evaluate whether estimates were different from zero. Prior to developing and running models, we examined correlation matrices of all pairwise combinations of covariates to identify any collinearity ($r > 0.5$) between explanatory variables. Correlations between all pairwise combinations of covariates were <0.24. We used Akaike's Information Criterion for model selection corrected for small sample size (AICc) to rank models and considered models with a $\Delta AIC < 2$ competing (Burnham and Anderson 2002). All values reported are means ± SE unless specified otherwise.

RESULTS

Nest Density, Size, and Overlap of Home Ranges. Average distance to nearest neighboring nest in the cluster of nests we studied was 698.1 ± 74.0 m (n = 15). Average sizes of home ranges of males (58.1 ± 9.58 ha, n = 8) were smaller than those of females (170.0 ± 15.4 ha, n = 8, paired t-test, $t_7 = 2.25$, $P = 0.059$), but average size of core areas did not differ between males (7.5 ± 2.8 ha, n = 8) and females (18.1 ± 7.3 ha, n = 8, paired t-test, $t_7 = 1.71$, $P = 0.131$). Proportion of overlap between home ranges of pair members differed by sex (n = 8, paired t-test, $t_7 = 2.53$, $P = 0.039$, Table 2), but proportion of overlap between core areas of pair members did not (n = 8, paired t-test, $t_7 = 1.56$, $P = 0.162$, Table 2). There was a large degree of overlap of home ranges of neighboring conspecifics, but core areas of neighboring conspecific males did not overlap (Table 2). The core area of one male and a neighboring female overlapped and the core area of one female overlapped with the core area of one neighboring female (Table 2). All home ranges of all males and females (n = 16), all core areas of females (n = 8), and all but two core areas of males (n = 6) contained the nest site from the previous breeding season. Average distance to the nest site from the edge of the core areas for the two exceptions was 85.1 ± 7.8 m. Distance between male and female hawks and their nest sites varied slightly (Fig. 1A, B), and average distance for males was 246.3 ± 11.6 m (n = 8) and for females 369.8 ± 28.6 m (n = 8).

Mate Interactions. Distance between pair members varied throughout the nonbreeding season (Fig. 1C). Members of a pair were, on average, closer

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Table 2. Average proportion of overlap between the home ranges and core areas of mated adult male and female Cooper's Hawks, males and neighboring conspecific males (Male: Male), males and neighboring conspecific females (Male: Female), females and neighboring conspecific males (Female: Male), females and neighboring conspecific females (Female: Female) during the nonbreeding season in Tucson, Arizona, 2010–2011.

	Proportion of Overlap					
	Home Range			Core Area		
Overlap Type	*n*	Mean	SE	*n*	Mean	SE
Mated pairs						
Male	8	0.790	0.084	8	0.710	0.099
Female	8	0.405	0.086	8	0.410	0.121
Conspecific neighbors						
Male: Male	8	0.438	0.057	0	0.000	0.000
Male: Female	7	0.870	0.237	1	0.020	0.000
Female: Male	7	0.418	0.100	1	0.001	0.000
Female: Female	6	0.919	0.139	2	0.001	0.001

to each other (473.4 ± 23.08 m, $n = 568$) than they were to random locations inside their home ranges (623.0 ± 22.07 m, $n = 568$) throughout the nonbreeding season (paired *t*-test, $n = 568$, $t_{567} = 11.6$, $P < 0.001$). Mate interactions ($n = 36$), including vocalizations between mates, acts of courtship, and feeding/perching while in close proximity, occurred throughout the nonbreeding season, and were common among all pairs we studied (i.e., six of the eight pairs engaged in at least two categories of interactions). Of the 36 observed mate interactions, 86.1% ($n = 31$) occurred inside core areas. Of the 31 interactions that occurred inside core areas, 93.5% ($n = 29$) occurred in areas of overlap between core areas of mated males and females. Average distance between mates in core areas was 313.3 ± 21.6 m ($n = 441$). Average distance between mates during interactions in core areas was 35.6 ± 3.9 m ($n = 31$).

Habitat Selection. A combination of distance to nest, proximity to the nearest core area of a neighboring conspecific, land-use type, a two-way interaction between sex and distance to nest, and a three-way interaction between proximity to the nearest core area of a neighboring conspecific, sex of the hawk selecting an area, and sex of the hawk occupying the neighboring core area was the most effective model for predicting relative probability of use (Tables 1, 3); there were no competing models. After controlling for availability of land-use types, selection of land-use types was not different for pair members, and compared to low-density residential areas, both pair members avoided agricultural areas, commercial areas, high-density residential areas, open spaces, roadways, and washes, but used recreation areas similarly (Fig. 2A). Distance to nest influenced the relative probability of using an area for both pair members, but more so for males (Fig. 2B). Influence of proximity to core areas of neighboring conspecifics on the relative probability of use varied by sex. For males, the relative probability of using an area was influenced strongly by proximity of neighboring conspecific males rather than females, and males had the highest relative probability of using an area at distances farthest from the core area of neighboring males (Fig. 2C). For females, proximity of neighboring conspecific of either sex did not strongly influence the relative probability of using an area, but females had the highest relative probability of using areas at distances farthest from the core area of neighboring females (Fig. 2D).

Discussion

The large degree of overlap in home ranges and core areas, strong territorially, fidelity to the breeding territory, and the interactions between mates suggests that mated pairs of Cooper's Hawks in Tucson maintained some level of pair bond throughout the nonbreeding season. Maintaining pair bonds outside the breeding season contrasts with behavior described in general for Cooper's Hawks (Snyder and Snyder 1991, Rosenfield and Bielefeldt 1993); however, perennial pair bonds in predatory birds may occur in environments that support year-round occupancy where prey resources are rich, and in species where both males and females occupy the same territory year-round (Newton 1979).

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Table 3. Coefficients ±95% HPD intervals of the most parsimonious generalized linear mixed-effects model predicting habitat selection within home ranges of mated adult male and female Cooper's Hawks during the nonbreeding season in Tucson, Arizona, 2010–2011. Estimates and HPD intervals are in comparison to reference level.[1,3,4]

		95% HPD INTERVAL	
VARIABLE	ESTIMATE	LOWER	UPPER
(Intercept)	0.623	0.382	1.147
Sex[1]	−0.902	−1.556	−0.621
Distance to nest	−0.387	−0.623	−0.237
NCA[2]	0.158	−0.101	0.456
NSex[3]	−0.389	−0.921	0.021
Distance to nest × Sex	−1.270	−2.009	−1.038
NCA × Sex	−0.073	−0.488	0.410
NCA × NSex	−0.102	−0.590	0.239
Sex × NSex	1.125	0.610	2.004
NCA × Sex × NSex	2.131	1.547	3.313
Land-use type[4]			
Agricultural lands	−2.022	−3.789	−1.310
Commercial property	−2.071	−3.240	−1.663
High-density residential	−0.635	−1.185	−0.328
Open space	−1.192	−2.458	−0.262
Recreation	0.774	−0.212	2.642
Roadways	−2.612	−4.060	−2.095
Washes	−1.762	−3.907	−0.653

[1] Reference level = "male."
[2] NCA = proximity to nearest core area of neighboring hawk.
[3] Nsex = sex of hawk occupying neighboring core area, reference level = "male."
[4] Reference level = "low-density residential."

Size of home ranges of female Cooper's Hawks during the nonbreeding season, although relatively small compared to Cooper's Hawks in undeveloped environments (Millsap et al. 2013), were larger than the home ranges of their mates. Use of comparatively large or different areas by female members of mated pairs during the nonbreeding season is common among *Accipiters*, as males are normally the territory holder and females are less restricted in their movements (Newton 1986, Millsap et al. 2013). Although female Cooper's Hawks ranged more widely compared to their mates, they frequently returned to the nest area and remained relatively close to their mates throughout the nonbreeding season. Distance between mates, however, may largely be a product of how far mates were from their nest site. The average distance a female was from her nest site closely corresponded to the average distance she was from her mate, likely because males remained uniformly close to the nest site throughout the nonbreeding season (see Fig. 1). Therefore, proximity to the nest site potentially governs the spatial relationship between pair members, and the nest site and surrounding breeding territory may serve as a rendezvous location for pair members. Courtship behavior (e.g., prey deliveries, vocalizations), for example, occurred throughout the nonbreeding season, but primarily within the area where core areas of pair members overlapped, which generally encompassed the nest site.

Within home ranges, pair members avoided all land-use types in comparison to low-density residential areas with the exception of recreation areas. This pattern of use is likely related to vegetation structure, hunting activities, and prey availability (Mannan and Boal 2000, Roth et al. 2008). In natural environments, Cooper's Hawks hunt in deciduous and coniferous forests (Rosenfield and Bielefeldt 1993). In Tucson, small groves of large nonnative trees (e.g., Aleppo pines, eucalyptus) are common in low-density residential and recreation areas, and the vertical structure of vegetation in these areas is similar to that in more natural habitat (Boal and Mannan 1998). Furthermore, in Tucson, residential and recreation areas support high abundances of many avian species (Boal 1997, Germaine et al. 1998), including Mourning Doves (*Zenaida macroura*), the second most abundant species in the city (Germaine et al. 1998), and a staple prey species of Cooper's Hawks in Tucson (Estes and Mannan 2003).

The perennial pair bonds of Cooper's Hawks and the deviation from the typical social behavior of mated pairs of Cooper's Hawks during the nonbreeding season could be a response to the high availability of prey in this urban environment. Urban areas can be very productive and support high densities of birds year-round because of abundant and reduced temporal variation in resources (Marzluff et al. 2001, Shochat et al. 2006). Food resources for birds also are often increased by supplemental feeding by humans (Chace and Walsh 2006, Robb et al. 2008). In Tucson, this creates an abundant and stable prey base and may have permitted pair members to occupy an all-purpose territory throughout the year (Boggie and Mannan 2014).

In an ecologically similar species, male and female Eurasian Sparrowhawks (*Accipiter nisus*) in the woodlands of Scotland are largely independent during the nonbreeding season, but exhibit moderately high rates of mate and site fidelity, particularly

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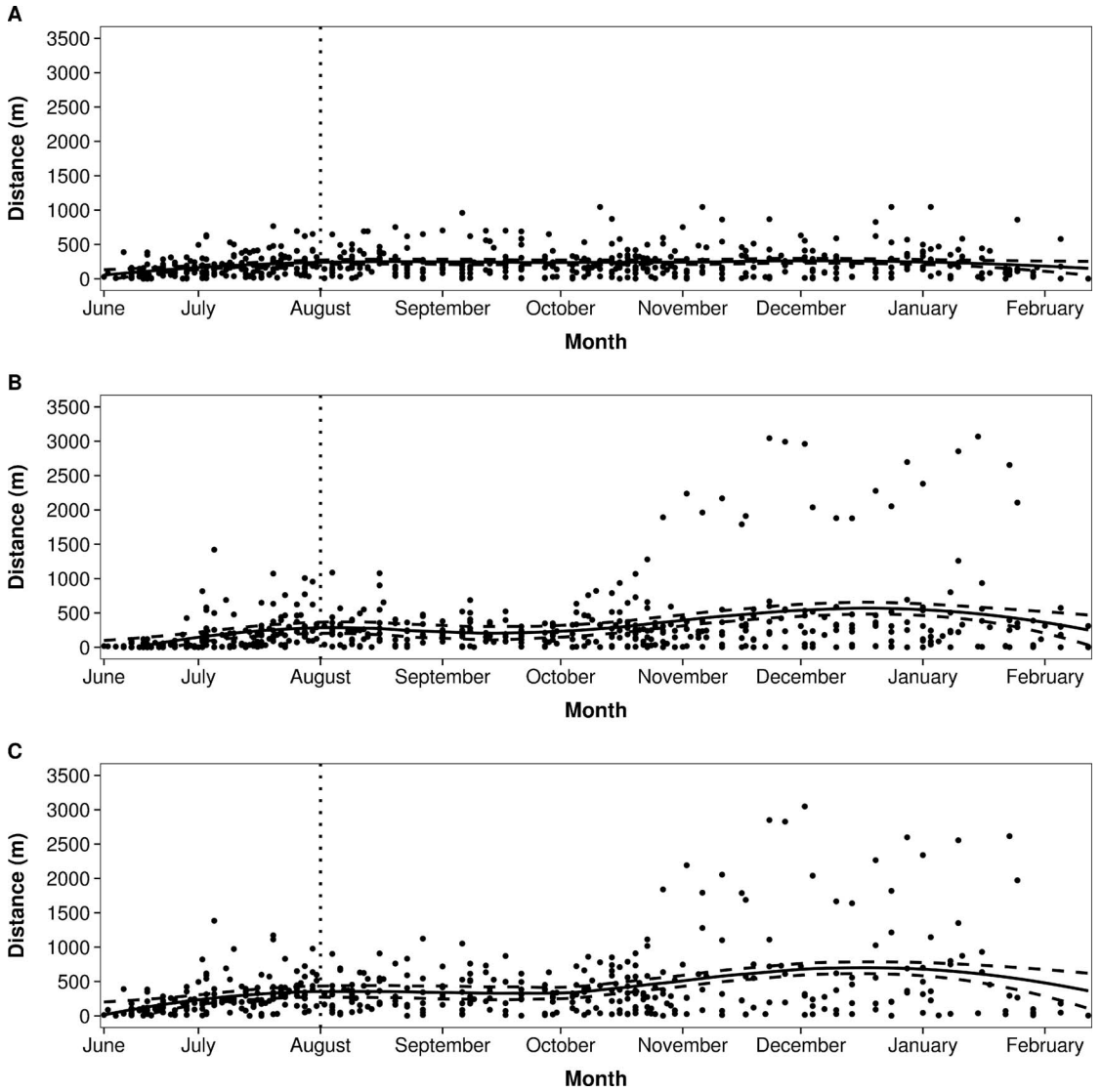


Figure 1. LOESS smoothed lines and dashed 95% confidence intervals for distances to nest for (A) adult male and (B) female Cooper's Hawks and (C) distances between adult mated male and female Cooper's Hawks as a function of month of the year in Tucson, Arizona, 2010–2011. Months to the left of the dotted vertical line represent the breeding season and months the right represent the nonbreeding season.

for older individuals and in areas and years when resources are abundant (Newton and Wyllie 1992). Male and female Cooper's Hawks in Tucson exhibit high site fidelity (96.6% and 90.6%, respectively, Mannan et al. 2007), and there is strong defense of sites against conspecifics. Territorially in Cooper's Hawks during the nonbreeding season appears to be strongest within sexes, a pattern that is common in other avian species (e.g., Slagsvold 1993, Appleby et al. 1999, Hall 2000). Defending a site during the nonbreeding season and interacting with a mate through forms of courtship may serve to prevent loss of a breeding site or a long-term investment in a mate (Penteriani 2001). Furthermore, mate fidelity and site fidelity are strongly correlated in many species and site fidelity may be a mechanism that drives mate fidelity in site-tenacious species (Mock and Fujioka 1990, Choudhury

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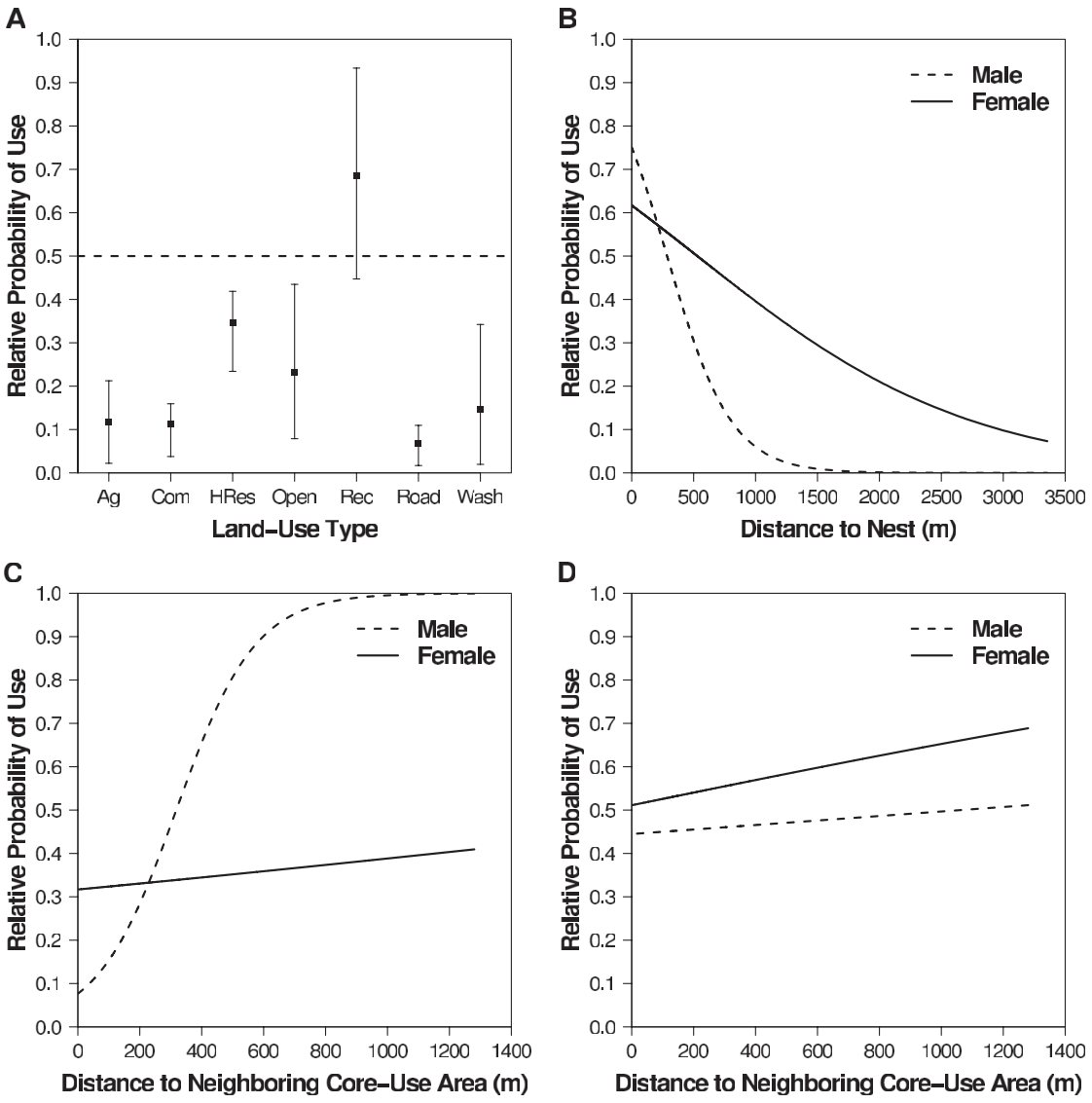


Figure 2. (A) Relative probability of use ±95% HPD intervals of a land-use type (Ag = agricultural lands, Com = commercial property, HRes = high-density residential, Open = open space, Rec = recreation, Road = roadways, Wash = washes) in comparison to the reference level low-density residential (dashed horizontal line designates where use is equal to availability; estimates and HPD intervals greater >0.5 were selected, estimates and HPD intervals <0.5 were avoided), (B) relative probability of use for mated males and females as a function of distance to a pair's previous year's nest site, and (C) relative probability of mated males and (D) females using an area as a function of sex of and proximity to the hawk occupying the nearest neighboring core area. Predicted from the best generalized linear mixed-effects model describing habitat selection within the home ranges of adult mated pairs of Cooper's Hawks in the nonbreeding season in Tucson, Arizona, 2010–2011. Variables not plotted were held constant at their mean values.

1995, Llambias et al. 2008, Bai and Severinghaus 2012). High mate fidelity and longevity of pair bonds in Cooper's Hawks in Tucson may be associated with high site fidelity.

There may be several adaptive advantages of maintaining pair bonds continuously throughout the year. First, the "mate familiarity effect" suggests that continual contact with a mate may improve

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coordination between a pair, thus increasing efficiency in breeding activities such as nest building, acquiring resources, and territory defense, all of which could improve breeding success (Black 1996, 2001, Van de Pol et al. 2006). Continual interaction also may allow females to assess the quality of their mates throughout the year (Kellam 2003). Second, both members of a pair may benefit from maintaining high mate fidelity over consecutive breeding seasons if it allows them to save time and energy that otherwise would be spent searching for and acquiring mates (Choudhury 1995, Cézilly et al. 2000). Also, maintaining pair bonds could allow them to initiate breeding earlier in the season and potentially increase breeding success (Fowler 1995, Boal and Mannan 1999). Among many species of predatory birds, for example, pairs that initiate breeding early often have higher reproductive success (e.g., Newton and Marquiss 1984, Sodhi et al. 1992, Margalida et al. 2007). Finally, in territorial species that exhibit high nest-site fidelity through multiple breeding seasons, females may stay with their mates because of high breeding success that comes with efficient acquisition of resources and territory defense (Newton and Wyllie 1992, Cézilly et al. 2000). All of these advantages are potentially realized for mated pairs of Cooper's Hawks in Tucson. Mated pairs of adult Cooper's Hawks, for example, that have nested for multiple breeding seasons in Tucson in the same territory have earlier hatch dates, larger broods, and fledge more nestlings than newly formed mated pairs of subadult females paired with adult males or subadult males (Boal 2001). Also, Cooper's Hawks in Tucson initiate nesting earlier and have larger clutch sizes than Cooper's Hawks occupying natural environments in southern Arizona, where they are thought to be solitary during the nonbreeding season (Boal and Mannan 1999). In this urban environment, mated pairs of Cooper's Hawks that have secured an all-purpose territory are able to occupy that territory and interact with their mate year-round, potentially strengthening their partnership and improving breeding efficiency. This likely translates into reproductive advantages over their nonurban counterparts.

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