

## TERRITORIALITY AND NEIGHBOR ASSESSMENT IN BROWN JAYS (*CYANOCORAX MORIO*) IN COSTA RICA

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**ABSTRACT.**—Defense of group-held resources is a common and widely accepted function of territorial interactions between neighboring groups. In addition, territorial interactions could provide opportunities to assess members of neighboring groups and reproductive opportunities there, or to solidify status in the home group. We studied group-level characteristics and individual participation in territorial encounters in the cooperatively breeding Brown Jay (*Cyanocorax morio*). Intergroup encounters at stable territory boundaries include both aggressive and affiliative behavior, which suggests that a territorial encounter could function as both a resource defense mechanism and as an arena for social interactions. Territory characteristics that increase the probability of contact between groups (long boundaries, large combined group size, and home range overlap) explain much of the variation in frequency of territorial encounters. Male-biased dispersal was more common to neighboring groups with long boundaries, supporting the idea that frequent interactions between neighbors facilitate dispersal. Females usually inherit breeding positions on their natal territories, and participation in intergroup encounters by females does not vary with age or breeding status. In addition to defending group resources, females on their natal territories could be defending their positions in the breeding queue. Immigrant females are not likely to breed successfully, or to disperse again, and they participated less than expected. Participation by both natal and immigrant males varied by age; young males, at the ages when dispersal and intergroup forays are most likely, participated more than expected, whereas older males ( $\geq 4$  years) participated less. That is consistent with the hypothesis that participation in intergroup encounters facilitates dispersal and improves integration into social groups. Because extragroup matings occur in this population, both breeding females and males could be assessing neighboring individuals for mating opportunities. Resource defense and social facilitation are not mutually exclusive hypotheses, and our observations suggest that both are important components of territorial encounters in Brown Jays. *Received 3 May 2002, accepted 25 November 2002.*

**RESUMEN.**—Una función ampliamente aceptada de la interacción territorial entre grupos vecinos es la defensa de los recursos que son mantenidos por el grupo. Además, las interacciones territoriales pueden proveer oportunidades para evaluar a miembros de grupos vecinos y oportunidades reproductivas, o para solidificar el estatus en el propio grupo. Estudiamos características a nivel de grupo y la participación individual en los encuentros territoriales en la especie de cría cooperativa *Cyanocorax morio*. Los encuentros entre grupos a lo largo de los límites territoriales estables incluyeron comportamientos agresivos y de afiliación, lo que sugiere que un encuentro territorial puede servir tanto como un mecanismo para la defensa de recursos como una arena para interacciones sociales. Las características de los territorios que aumentan la probabilidad de contacto entre grupos (límites largos, gran tamaño de grupo combinado y coincidencia de los rangos de hogar) explican gran parte de la variación en la frecuencia de encuentros territoriales. La dispersión sesgada hacia los machos fue más común entre grupos con fronteras largas, lo que confirma la idea de que las interacciones frecuentes entre vecinos facilitan la dispersión. Las hembras generalmente heredan posiciones de cría en sus territorios natales y la participación de las hembras en encuentros grupales no varía con la edad ni con el estatus reproductivo. Además de defender los recursos del grupo, las hembras que se encuentran en sus territorios natales podrían también estar defendiendo su oportunidad para criar. Las hembras inmigrantes presentan una probabilidad menor de reproducirse con éxito o de dispersarse nuevamente y participaron menos de lo esperado. La participación de los machos nativos e inmigrantes varió con la edad; machos jóvenes, de edades a las cuales la dispersión e incursiones intergrupales son más probables, participaron más de lo esperado,

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mientras que machos de mayor edad ( $\geq 4$  años) participaron menos. Esto es consistente con la hipótesis de que la participación en encuentros intergrupales facilita la dispersión y mejora la integración en grupos sociales. Debido a que apareamientos extragrupalos ocurren en esta población, tanto las hembras como los machos podrían estar evaluando a los individuos vecinos como oportunidades de apareamiento. La defensa de los recursos y la facilitación social no son hipótesis mutuamente exclusivas y nuestras observaciones sugieren que ambas son componentes importantes en los encuentros territoriales de *C. morio*.

MOST COOPERATIVELY BREEDING birds defend group territories whose boundaries remain relatively stable from year to year, with the exception of a few colonial species (Brown 1987, Stacey and Koenig 1990, Emlen 1991). Territorial defense has often been assumed to be an aggressive behavioral response to competition over limited, defensible resources (Brown 1964, Waser and Wiley 1979, Stamps 1994). Studies of cooperatively breeding birds have identified a variety of defensible ecological resources such as cover for nesting or nest cavities (Craig 1980, Walters 1990), space that can be passed on to descendents (Woolfenden and Fitzpatrick 1978, 1984; Brown and Brown 1984), and food resources (Koenig and Mumme 1987, Langen and Vehrencamp 1998). Another class of resources includes mates and maintenance of stable breeding queues (Wiley and Rabenold 1984, Rabenold 1990).

Although it has received less attention, territorial encounters may have other functions in addition to resource defense. Stamps (1994) has emphasized that territorial behavior may not always have an aggressive or competitive function. Interactions with neighbors could also be attempts to elicit information or form social bonds. In social animals, individuals could use territorial encounters as a way to gain information on availability of breeding opportunities with neighboring individuals or to form social bonds that would subsequently facilitate dispersal and acquisition of mates (Zack 1990, Lazaro-Perea 2001). Individuals might also gain benefits through status signaling and enhancement of their standing within their social group (Zahavi 1977, 1990).

Studies of social animals lend support to those alternative possibilities. In Stripe-backed Wrens (*Campylorhynchus nuchalis*), participation in territorial encounters allows females to assess availability of breeding openings in neighboring groups, and information gained from such assessments probably confers an advantage in contests for breeding positions in a familiar group (Zack and Rabenold 1989, Zack 1990,

Yaber and Rabenold 2002). Territorial behavior of Tasmanian Native Hen (*Gallinula mortierii*) groups normally serves as a means of assessing condition of neighboring groups and availability of breeding opportunities (Putland and Goldizen 1998). Territorial encounters can also serve to integrate individuals within their own social unit. In Florida Scrub-Jays (*Aphelocoma coerulescens*), active participation in territorial defense may be a prerequisite for territory inheritance by male offspring (Woolfenden and Fitzpatrick 1977, 1978). In primates, both aggressive and affiliative behaviors are observed between groups during territorial encounters, which suggests that individuals are using those encounters to become familiar with and assess neighboring individuals (French et al. 1995, Perry 1996, Lazaro-Perea 2001). In most primate species characterized by male dispersal, young males in their natal groups are the most active participants in intergroup encounters, and such interactions precede and potentially facilitate their subsequent transfer to other groups (Cheney 1987).

Here, we asked if variation in territorial encounters among groups of Brown Jays (*Cyanocorax morio*) is related to group size and spatial configuration of territories and discuss how that might affect intergroup relationships. We also asked if territorial encounters could be used by individuals to assess and become familiar with neighboring individuals, or to facilitate integration into a new group, as well as to defend resources. We predicted that, if the latter two additional functions pertained, the age-sex classes most prone to dispersal would participate most in territorial encounters.

## METHODS

*Study area and population.*—The study area is ~4 km<sup>2</sup> in Monteverde, Puntarenas (10°15'N, 84°46'W), at an elevation of 1,400–1,500 m on the Pacific slope of the Cordillera de Tilarán in Costa Rica (Fig. 1). It lies on a plateau bounded on the east by a large expanse of cloud forest, and on the south and west by cliffs; it receives ~2,500 mm of rain annually. Monteverde is

composed of considerable remnant premontane and lower montane moist-wet forest (Holdridge 1967), windbreaks, pastures, orchards, and gardens (Lawton and Dryer 1980, Lawton and Lawton 1985, Nadkarni and Wheelwright 2000).

Brown Jays live in large groups ( $\bar{x}$  = 10 individuals), within which most individuals are nonreproductive "helpers" (Skutch 1960, Lawton and Guindon 1981, Lawton and Lawton 1985). Members of groups associate consistently within a shared home range area ( $\bar{x}$  = 14 ha) consisting of pasture and forest. Most groups are known to have occupied those same home ranges since 1988 and group members collaborate in building nests, feeding incubating females, and feeding and defending nestlings and fledglings. Whereas most Brown Jay groups contain a single breeding female, 29% contain two to three breeding females with separate nests. Successful reproduction, however, is normally limited to one female per group. Survivorship of adults is high (86% yearly survival). Dispersal and temporary intergroup visiting, which usually precede dispersal by a year or two, is male-biased within the population (2.7 males:1 female), and most dispersal occurs at two to three years of age (Williams 2000). For both males and females, dispersal is almost always (96%) to an adjacent territory and is rarely in response to an obvious breeding vacancy; instead, individuals must often wait several years in their new group before breeding. Behavioral observations and DNA fingerprinting results indicate that a single female is the mother of all the young in her nest and that females commonly mate with males that are not their "social" mate (consort). Multiple paternity

occurs within 43% of broods. Males within the social group father most of the nestlings, whereas 30% of nestlings represent extragroup paternity (Williams 2000). Older individuals of both sexes (>4 years old) are more likely to become breeders. Group size is not positively related to the production of young in the population (Williams et al. 1994, Williams 2000). The major route to fitness for females in this population appears to be through inheritance of a breeding position on the natal territory, whereas males gain breeding opportunities mainly through dispersal and extragroup matings.

All nestlings in the study area have been banded with unique combinations of colored aluminum bands since 1988, and genetically sampled since 1992. Adults have been captured in box traps and mist nets since 1994. In 1996, 84% of adults were banded (of 149 individuals) in 15 social groups. All unbanded adults were identified based on unique patterns of yellow and black on their eye-rings, beaks, and legs (see Skutch 1960, Lawton and Lawton 1985, Williams et al. 1994). We knew the natal origins of 62% of the individuals in the population by 1996 (92 of 149 individuals). Brown Jays are sexually monomorphic to the human eye, so all genetically sampled individuals were sexed using the PCR-based approaches developed by Griffiths et al. (1998) and Kahn et al. (1998). We could determine sex of some unsampled individuals if they engaged in consort behavior (males) or nested (females), because those two behaviors were always correlated with genetic determination of sex (Williams 2000).

Females were classified as breeders (those that built nests) or as natal and immigrant nonbreeders. Males were classified as consorts of a nesting female (those that helped the breeding female build her nest and followed her during egg laying and incubation, that is, her social mate) or as natal and immigrant males (those that did not engage in consort behavior). Because actual genetic parentage varies among years for individual males and is not strongly correlated with consort status, we could not classify all males as breeding versus nonbreeding. Jays classified as young were one year old. Intermediate age class included two and three year old jays banded as nestlings and jays of unknown age that had been identified for two to three years. Old age class included jays that were more than three years old and banded as nestlings and jays of unknown age that had been identified for at least four years. Immigrants were individuals in a social group that were known to have been born in another territory through banding records or unbanded adults that were not with their current social group in previous breeding seasons.

*Behavioral observations of territorial encounters.*— From March–July 1996, A.M.H. conducted 2 h focal observations, controlling for time of day and stage in the breeding season, of each group approximately ev-

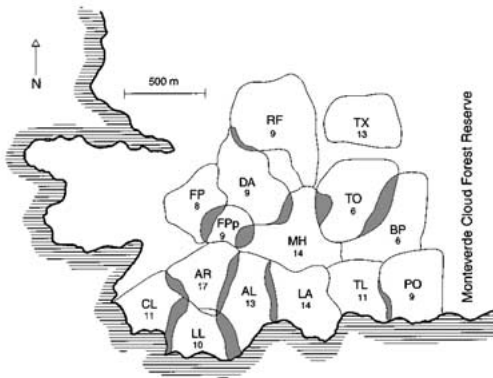


FIG. 1. Map of the Brown Jay study area in Monteverde, Costa Rica in 1996. The heavy black line with shading around the south and west sides represents the cliff edge. The thin black lines represent home range boundaries. Areas of overlap between home ranges are shaded gray. The focal group sizes are shown within territory boundaries. Nonfocal Brown Jay groups surround the study population on the southern, western, and northern sides.

ery two weeks (Altmann 1974). After locating a group, she followed it throughout the territory, recording all encounters between groups. If a group was already involved in an encounter when located, then the onset of the encounter was recorded as the beginning of the focal observation. We determined an encounter to be over when either or both groups returned to their territories. All focal observations were terminated at the end of two hours, regardless of intergroup activity.

The following information was collected during intergroup encounters: duration and location of encounter, identity of participants, stage during breeding season for each involved group, and types of behaviors observed. An individual participant was scored only once for each intergroup encounter (participated or not). It was not possible to conduct focal animal observations during those encounters or to determine identity of all individuals involved in specific types of behaviors. Individuals scored as participating were observed performing at least one behavior characteristic of an intergroup encounter. We did not observe individuals simply sitting and not interacting in those encounters. Individual participation was analyzed for only 12 of the 15 social groups because habitat characteristics for three of those groups made it very difficult to identify participants reliably. For the small number of cases in which we were able to identify all of the participants in a particular interaction (e.g. head bobbing between two individuals), we recorded particular behaviors associated with those individuals. We have no evidence from census data or focal observations that certain classes of individuals are more conspicuous to an observer than others.

The frequency and duration of encounters were standardized for each focal group by dividing those measures by focal observation-hours for each group. Although not included in calculation of interaction rates, *ad libitum* observations (by A.M.H. and D.A.W.) of intergroup encounters were recorded throughout the breeding season.

*Determination of home range and territory characteristics.*—The study area was completely censused before the breeding season (early February) and at the end of the breeding season (July–August) in 1994–1996 (16 groups in 1994 and 1995, and 15 groups in 1996). Each group was followed and its location recorded for a minimum of 20 h each year during censusing of individuals over an average of nine days. In addition, group locations and individual identities were noted during numerous visits to check nest contents, conduct focal nest observations, and trap individuals within each group. We made a detailed map of home-range boundaries from a 1992 aerial photograph and ground measurements by enclosing all areas in which a group was seen foraging or resting throughout the entire breeding season (Fig. 1). Territory boundaries enclose the exclusively occupied area by each social group (i.e. home range area minus area of overlap with neighbors (Fig. 1). Males sometimes

briefly visited adjacent groups during the breeding season (Williams 2000), but those movements were not considered in the construction of home-range and territory boundaries. Visiting individuals usually did not participate in a group's activities except occasionally to feed nestlings. Visitors always returned to their origin group where they were seen to participate in helping and territorial encounters on a regular basis.

Total home-range area (territory area plus overlap area) for each group was determined using the Geographical Information System (GIS) ARC/INFO and ARCVIEW (version 3; Environmental Systems Research Institute, Redlands, California). We also measured nearest concurrent nest-to-nest distances across boundaries, length of shared boundaries between adjacent groups, and nearest nest-to-boundary distances for each group from the maps we constructed.

*Statistics.*—Statistical analyses were performed in MINITAB (version 12.22; Minitab Inc., State College, Pennsylvania). Variables were transformed as needed before performing parametric statistical tests. In those cases where data sets clearly deviated from assumptions of normality and constancy of error terms, the data were ranked and Spearman rank correlations (correlation coefficient presented as  $r_s$ ) were used to analyze the data. Group-pair interaction rates were rank-transformed before using conventional parametric statistical methods (Conover and Iman 1981). Means and standard errors are presented, unless otherwise noted. All probabilities are two-tailed. We used chi-square tests (goodness-of-fit tests) to analyze frequency of participation in territorial encounters by individuals of different sex, age, social, and dispersal-status categories and to analyze frequency of dispersal across long (200 m or greater) and short (<200 m) territorial boundaries. For each chi-square, we calculated expected number of territorial encounters or dispersal events for each category based on that category's proportional representation within the 12 social groups or study area. We applied Yates correction for continuity to chi-squares with one degree of freedom.

## RESULTS

*Territorial encounters.*—Intergroup encounters in Brown Jays can last from 10 min to 3 h (modal duration = 30 min). On average,  $9.7 \pm 4.6$  (SD) total individuals or  $44.9\% \pm 18.9$  (SD) of the total combined group members were involved in territorial encounters ( $n = 73$  encounters). Aggressive behaviors were common in intergroup encounters, including aerial chasing between individuals from different groups, often accompanied by harsh "chirring" calls. Head bobbing (quickly raising and lowering

the head) and posturing (sleeked plumage in a vertical body position with bill held high and tail low, or in a horizontal crouch) between two or among three individuals were often followed by chases through vegetation. Chasing, head bobbing, and posturing are recognized aggressive behaviors (Hardy 1974, Alvarez 1975) and were seen in 91% of encounters ( $n = 70$  of 77 focal and nonfocal encounters). Those behaviors were followed by contact fighting (pecking and grappling with the feet) in 31% ( $n = 24$ ) of encounters. Several affiliative displays that we often observed between individuals within social groups were also observed in intergroup encounters. One of those, termed "up-fluffing" (Hardy 1974, Lawton and Lawton 1985), was seen in 27% ( $n = 21$ ) of territorial encounters. It involves two or more individuals sitting next to each other with extended necks and erected feathers on head and neck. This behavior suggests solicitation of preening because it was usually followed by one individual looking closely at the other individual's neck and sometimes gently probing the erected feathers with the beak. In 10 cases of up-fluffing during territorial encounters when both participants could be identified, they were from separate groups. "Flight displays" were seen in 55% ( $n = 42$ ) of territorial encounters and involved four or more jays flying together in a long swooping flight between two trees separated by 50–100 m while giving loud rapid calls. Individuals then perched silently before repeating the process 2 to 10 $\times$  between the same trees. Chasing rarely occurred during this display and individuals did not interact with each other after landing.

Territorial encounters occurred throughout the breeding season. An encounter occurred every 4.5 h of focal observation during the early stages of breeding ( $n = 21$  encounters) (pre-nest building, nest building, egg laying) and every 6.2 h during later stages ( $n = 34$ ) (incubation, nestling, fledgling) ( $\chi^2 = 1.22$ ,  $df = 1$ ,  $P > 0.1$ ). The mean duration of encounters observed for their entirety during the early stages of breeding ( $\bar{x} = 76.3 \pm 11.2$  min,  $n = 19$ ) was greater than during the later stages ( $\bar{x} = 48.8 \pm 6.4$  min,  $n = 33$ ) ( $t$ -test,  $t = 2.31$ ,  $df = 50$ ,  $P = 0.03$ ).

*Variation in territorial encounters among groups.*—Frequency and proportion of time groups spent in territorial encounters may have been correlated with group size ( $r = 0.49$ ,  $0.48$ ;  $P = 0.07$ ,  $0.07$  respectively,  $n = 15$ ), but not with the

number of surrounding groups ( $r = 0.10$ ,  $0.10$ ;  $P = 0.71$ ,  $0.72$ , respectively,  $n = 15$ ) or home-range area ( $r = -0.07$ ,  $-0.05$ ;  $P = 0.79$ ,  $0.86$  respectively,  $n = 15$ ). Length of the boundary between pairs of interacting groups ( $n = 25$ ) was positively correlated with frequency and proportion of time spent in territorial encounters with each other (Fig. 2). Because of the high correlation between boundary length and likelihood of interaction between a particular pair of groups, the interaction rates were standardized by dividing them by length of the shared boundary (in meters). The standardized interaction rates clearly deviated from normality; therefore, we used ranked, standardized interaction rates in all subsequent analyses. Several significant correlations were found between the standardized boundary interaction rates and neighboring group characteristics (Table 1). Territorial encounters occurred with greater frequency and lasted longer for group-pairs with home-range overlap (Wilcoxon test,  $H_1 = 4.45$ ,  $7.75$ ;  $P = 0.04$ ,  $0.005$ , respectively;  $n_1 = 12$ ,  $n_2 = 13$ ). Boundary habitat type (forest or open edge) did not affect either the proportion of time spent in encounters or the frequency of encounters (Wilcoxon test,  $H_1 = 0.67$ ,  $1.25$ ,  $P = 0.41$ ,  $0.35$ , respectively,  $n_1 = 9$ ,  $n_2 = 16$ ).

We considered combined group size, relative group size, nest–nest and nest–boundary distances, and home-range overlap as possible factors in a multivariate model of ranked group-pair interaction rates. We included all possible combinations of explanatory variables that were not colinear in multivariate ANCOVA and ANOVA models. No interaction among explanatory variables was significant. Controlling

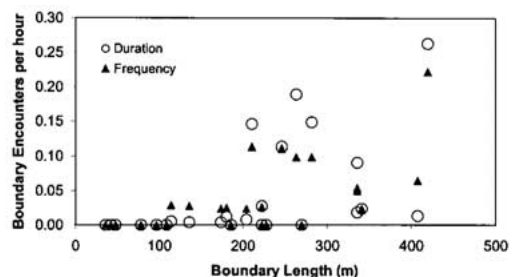


FIG. 2. Frequency and duration (proportion of observation time spent in territorial encounters) of Brown Jay territorial encounters increase with boundary length ( $r = 0.62$ ,  $0.53$ ;  $P = 0.001$ ,  $0.007$ , respectively;  $n = 25$ ).

TABLE 1. Spearman correlation ( $r_s$ ) table of the relationship between the standardized boundary interaction rates (see text) and neighboring group characteristics (1996) ( $n = 25$ ).

Territorial encounters	Combined group size	Relative group size	Nest-boundary distance (m)	Concurrent nest-nest distance (m)
Proportion of observation time	0.45*	-0.07	-0.49**	-0.41*
Frequency	0.34	-0.07	-0.51**	-0.40*

\* $P < 0.05$ ; \*\* $P \leq 0.01$ .

for boundary length, proportion of time spent in encounters was greatest for large group-pairs with home-range overlap (ANCOVA, total individuals,  $MS = 172.18$ ,  $F = 5.82$ ,  $df = 1$  and  $22$ ,  $P = 0.025$ ; overlap,  $MS = 316.85$ ,  $F = 10.7$ ,  $df = 1$  and  $22$ ,  $P = 0.003$ ), and encounters were most frequent for group-pairs with home-range overlap (one-way ANOVA, overlap  $MS = 225.36$ ,  $F = 5.23$ ,  $df = 1$  and  $23$ ,  $P = 0.03$ ).

We compared number of dispersal events across boundaries 200 m or greater in length (the point of increase in territorial encounters,  $n = 16$  boundaries; Fig. 2) to those across shared boundaries shorter than 200 m ( $n = 13$ ), for all recorded dispersal events between 1991 and 1998, predicting that dispersal would be more common across longer boundaries if intergroup social interactions facilitated dispersal. Rather than construct a null expectation based on geometric considerations of the expected result of random movements (more movement across longer lines on a map), it seemed more biologically meaningful to construct a null that incorporates the realism that jays are not likely to be attracted to a long boundary because of its geometric properties, but rather to a group with relevant characteristics, like familiarity. The null expectation in our analysis of dispersal events is that jays will disperse without regard to familiarity with a particular group, as represented by boundary length. If the null were supported, dispersal would be distributed among short-boundary and long-boundary (familiar) groups in proportion to their representation in the study area. In fact, significantly more dispersal occurred between groups with shared boundaries 200 m or greater ( $n = 41$  dispersal events; 29 males and 6 females) than between groups with shorter shared boundaries ( $n = 11$  dispersal events; 9 males and 2 females) ( $\chi^2 = 10.83$ ,  $P = 0.001$ ). Individuals often disperse jointly with other group members and so we repeated the same analysis treating each

joint dispersal as one event. Individuals still disperse more frequently across long territory boundaries ( $n = 28$  dispersal events) than short boundaries ( $n = 7$  dispersal events) ( $\chi^2 = 7.76$ ,  $P = 0.005$ ). Two of three extragroup fathers that were identified (Williams 2000) were also from groups that shared long boundaries with the neighboring group where they obtained matings. In 1998, some of the males and females that were observed in territorial encounters with neighbors in 1996, when behavioral observations were made, had subsequently become members of neighboring groups with which they interacted frequently. Nine of those 10 dispersals were across long boundaries (200 m or greater) ( $n = 6$  of 37 males and 4 of 35 females observed in 1996 and still living in 1998). Three of the males became consorts of nesting females in the years following 1998 and one female became a primary nesting female.

*Individual participation in territorial encounters.*—Individuals differed in their participation in territorial encounters based on sex, breeding, and dispersal status ( $\chi^2 = 31.4$ ,  $df = 5$ ,  $P < 0.0001$ ) (Fig. 3). Natal males and immigrant females participated less than expected, whereas immigrant males participated more than expected. Both males residing on their natal territories and immigrant males differed by age in their participation in territorial encounters ( $\chi^2 = 15.6$ ,  $df = 2$ ,  $P = 0.0004$ ;  $\chi^2 = 6.3$ ,  $df = 1$ ;  $P = 0.01$ , respectively; Figs. 4 and 5). Young and intermediate aged (1–3 years old) males participated in more encounters than expected, while old ( $\geq 4$  years old) male jays participated in fewer encounters than expected. Females in their natal territories did not differ by age class in participation in territorial encounters ( $\chi^2 = 3.85$ ,  $df = 2$ ,  $P = 0.15$ ; Fig. 4).

We were able to identify all of the participants in 44 interactions during intergroup encounters: 37 between two individuals, 5 among three individuals, and 2 among four individuals. There was no evidence that interactions were

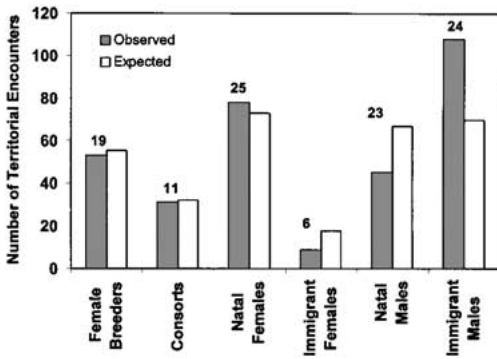


FIG. 3. The observed and expected number of territorial encounters for Brown Jay individuals of different breeding and dispersal classes ( $\chi^2 = 31.4$ ,  $df = 5$ ,  $P < 0.0001$ ; Individual contribution of each category to overall chi-square value: female breeders = 0.28, consorts = 0.12, natal females = 0.12, natal males = 8.35, immigrant males = 18.0, immigrant females = 4.5). The numbers above the bars represent the number of individuals in each class.

predominantly intrasexual; males and females interacted with their own and opposite sex at expected levels ( $\chi^2 = 0.08$  and  $0.79$  respectively,  $df = 1$ ,  $P > 0.1$ ; Table 2). Aggressive display behaviors were the most common (59%) type of interaction, followed by up-fluffing (23%) and contact fighting (18%).

#### DISCUSSION

For Brown Jays, both resource defense and affiliative social interaction appear to be important components of intergroup encounters. Intergroup encounters occurred along stable boundaries and aggressive behaviors were common, which suggests that individuals were defending group-held resources or the social integrity of the group. The majority of territorial encounters involved agonistic display behaviors (head bobbing and posturing) and chasing. Contact fighting occurred during territorial encounters, but typically very few individuals were involved in this potentially dangerous escalation. Territorial encounters also included nonaggressive behaviors, which suggests that individuals were engaged in more than resource defense (see also Lazaro-Perea 2001). The solicitation of allopreening in birds and allogrooming in primates (appeasement behavior that may have originally evolved to reduce aggression) currently functions to promote group cohesion

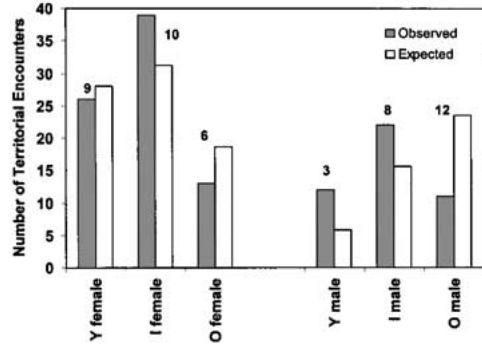


FIG. 4. The observed and expected number of territorial encounters for different age classes (Y, 1 year; I, 2-3 years; O,  $\geq 4$  years) of non-breeding natal females ( $\chi^2 = 3.85$ ,  $df = 2$ ,  $P = 0.15$ ) and natal males ( $\chi^2 = 15.61$ ,  $df = 2$ ,  $P = 0.0004$ ; Individual contribution of each category to overall chi-square value: Y = 6.40, I = 2.58, O = 6.63). The numbers above the bars represent the number of individuals in each class.

and social bonding among individuals in social species (Harrison 1965, Sparks 1967, Hardy 1974, Gaston 1977, Lawton and Lawton 1985). For instance, up-fluffing occurs commonly among all individual Brown Jays in a flock and can occur both when individuals first come into contact and after individuals have been sitting together for long periods of time. Although we cannot completely discount the possibility that up-fluffing may have occurred as an appeasement display during intergroup encounters (see Lawton and Lawton 1985 for an example),

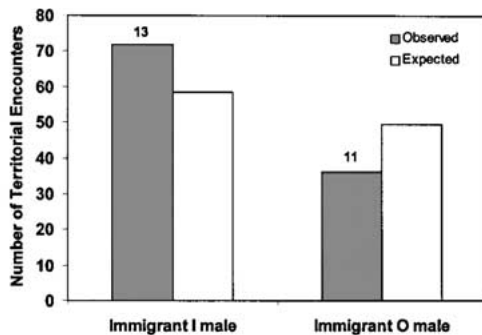


FIG. 5. The observed and expected number of territorial encounters for different age classes (I, 2-3 years; O,  $\geq 4$  years) of immigrant male Brown Jays ( $\chi^2 = 6.30$ ,  $df = 1$ ;  $P = 0.01$ ; individual contribution of each category to overall chi-square value: I = 3.12, O = 3.68). Numbers above bars represent the number of individuals in each class.

TABLE 2. Number and type of behaviors seen in interactions between identified individuals during Brown Jay territorial encounters.

	Agonistic	Contact		Total
	display	Fighting	Up-fluffing	
Male-male	14	5	2	21
Male-female	8	3	4	15
Female-female	4	0	4	8
Total	26	8	10	44

up-fluffing was not preceded or followed by aggressive behaviors in intergroup encounters we observed. The function of the flight display is not clear, but it appears analogous to other group displays such as group vocalizations and displays in Noisy Miners (*Manorina melanocephala*; Dow 1975), and duets often linked to joint flights in *Campylorhynchus* wrens (Rabenold 1990), which probably function to promote group cohesion and social bonding. We believe that the presence of those two displays in intergroup encounters suggests that individuals are not only engaged in agonistic resource defense behaviors, but are also engaging in the process of social bonding that could lead to assessment of mates, successful dispersal, and integration into a new group.

Several studies have suggested that the basic geography and geometry of neighboring territories can cause variation in territorial defense simply by altering the probability of contact between neighbors (Hamilton et al. 1976, Stamps et al. 1987). Here, the frequency and proportion of time spent in territorial encounters appeared to be directly related to the configuration of territory boundaries and to the increased opportunity for interaction with increasing numbers of individuals. If social interactions and familiarity facilitate dispersal by males, then we should expect that neighbors with longer shared boundaries would exchange more dispersers than neighboring groups with shorter boundaries. That prediction is supported by our data and may explain, in part, why some pairs of groups have tended to exchange more dispersers than others (Williams 2000). In addition, we have found that males tend to disperse to groups where relatives have also dispersed before them (D. A. Williams and K. N. Rabenold unpubl. data). We suggest that variables that increase the probability of contact between two neighboring groups (e.g. territory geometry, nest placement, and group size) could influence

dispersal movements and cross-group breeding, especially in species that require an extended period of social interactions to form alliances or social bonds.

The value of critical resources and costs of defense (energetic, loss of foraging time, increase in predation risk, risk of injury) can differ among group members (Waser and Homewood 1979, Brown 1987, Mares and Lacher 1987, Heinsohn and Packer 1995). Other studies of cooperative breeding birds have demonstrated that individuals invest more in territorial defense when the territory represents an immediate or future breeding opportunity. Breeders put more effort into territorial defense than helpers in Acorn Woodpeckers (*Melanerpes formicivorus*; Mumme and de Queiroz 1985) and Tasmanian Native Hens (Putland and Goldizen 1998). Males are the philopatric sex in Galápagos Mockingbirds (*Nesomimus parvulus*; Kinnaird and Grant 1982), Florida Scrub-Jays (Woolfenden and Fitzpatrick 1977, 1986), and Groove-billed Anis (*Crotophaga sulcirostris*; Vehrencamp 1978, Bowen et al. 1989) and they participate in territorial defense more than females.

Most female Brown Jays obtained breeding positions in their natal territories (Williams 2000) and both breeders and helpers participated often in territorial defense. Participation in territorial encounters did not differ by breeding status or age class for natal females, which suggests that immediacy of breeding does not motivate individuals to participate more. Breeding and nonbreeding females may be defending group resources and protecting their place in the breeding queue by discouraging more immigration. Breeding females may also be assessing extragroup mating opportunities. Immigrant females participated less than expected in territorial encounters and that may be because the territory does not represent a direct or high-quality breeding opportunity for those individuals. Females that have dispersed and obtained breeding positions experience lower breeding success than females breeding on their natal territories (Williams 2000).

Male Brown Jays did not often obtain breeding positions in their natal territories (Williams 2000), which may explain the lower level of participation by older natal males. Nevertheless, the natal territory does represent a valuable nonbreeding resource for males. The natal territory is a staging ground for forays into neighboring

groups and territorial encounters provide an opportunity for neighbor assessment. Young and intermediate aged natal males participated more than expected in territorial encounters. Those ages coincide with modal ages of intergroup forays and dispersal, which suggests that those males are familiarizing themselves with neighbors prior to dispersal. Intergroup forays precede dispersal by one to a few years and are also consistent with the idea that familiarization with neighbors facilitates dispersal (Williams 2000). We do not know why older natal males participated in intergroup encounters less than expected, because one might expect that those individuals would be motivated to disperse and would benefit by interactions with neighboring groups. Those individuals may represent individuals that never attempt breeding (as in Florida Scrub-Jays; Fitzpatrick and Woolfenden 1989), or they could be engaged in cross-group or intragroup mating strategies for which their status is well established.

Immigrant males of intermediate age participated in significantly more intergroup encounters than expected. Participation in group activities such as territorial defense could be a means of increasing status and facilitating integration into the group for those individuals (Zahavi 1977, 1990). Recent male immigrants could also be familiarizing themselves with new neighbors because secondary dispersal and cross-group matings occur. The fact that both younger immigrant males and younger natal males exhibited similar participation suggests that those ages represent a critical time for males to disperse and become integrated into a breeding group. Male immigrants could also be protecting their place in the breeding queue by discouraging more immigration or extragroup matings. There was no indication, however, that interactions were predominantly intrasexual and participation was not greater in older females and immigrant males who are closer to breeding and potentially might have more to lose from immigrants. Furthermore, males also make intergroup forays, often without apparent aggression from other group members. Breeding females also obtained extragroup matings (Williams 2000). Nevertheless, most breeding does occur within groups so that males could still be able to discourage some individuals from immigrating. Both breeding females and older immigrant males could also be assessing

extragroup mating opportunities. The longer duration of territorial encounters during early stages of breeding is consistent with the possibility that individuals are assessing potential mates. Male forays into neighboring groups also occur at a greater frequency during that time (Williams 2000). Our measure of participation is too crude to tease apart the relative importance of resource defense versus neighbor assessment to different classes of individuals. In the future, it will be important to conduct more detailed behavioral observations of those encounters on fewer groups to better quantify types of interactions among classes of individuals.

Our data support the hypothesis that territorial encounters can serve multiple functions in social animals. We suggest that resource defense is not the only function of territorial behavior in Brown Jays. Intergroup encounters allow individuals to sample neighboring group membership and gain information about dispersal and reproductive opportunities in the neighborhood, as well as to possibly promote their status in the home group.

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