The effect of local dominance and reciprocal tolerance on feeding aggregations of ocellated antbirds

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We studied ocellated antbirds (*Phaenostictus mcleannani*) to test the hypothesis that reciprocal tolerance between dominant individuals can favour feeding in aggregations. Mated pairs hold large non-exclusive feeding ranges, but roost and nest in a small portion of this range ('roosting area'); adjacent roosting neighbours are unrelated. Ocellated antbirds congregate to feed on arthropods fleeing from nomadic swarms of army ants that move across the ranges of many pairs. We used playback experiments to simulate acoustic challenges, and results showed that males responded aggressively to other males only in their roosting areas. Responses to adjacent neighbours were less aggressive than to non-neighbours (i.e. the 'dear enemy' effect). Prey intake rates were higher when birds fed in their own roosting area or in that of adjacent neighbours compared with more distant sites. Males tolerated adjacent neighbours at swarm fronts where prey are most dense, but more distant neighbours were displaced. Despite small samples for some analyses, our results suggest that reciprocal tolerance between adjacent unrelated neighbours can ameliorate intraspecific competition within ephemeral feeding aggregations.

Keywords: army-ant-following; dear enemy; playback; reciprocity; territoriality

1. INTRODUCTION

Animals that aggregate to feed should balance the costs of feeding with conspecifics (e.g. competition for food) against the benefits obtained from interactions with related or unrelated individuals (Krause & Ruxton 2002; Covas & Griesser 2007). The balance between costs and benefits of feeding in aggregations can be affected by dominance status (Ekman 1987; Krams 1998; Krause & Ruxton 2002). Here we focus on benefits obtained from interactions between unrelated conspecifics that are mediated by site-specific dominance. Many of the species that form feeding aggregations are non-territorial, whereas others exhibit some degree of site-specific dominance. In the latter, each individual enjoys priority access to food in part of its feeding range without defending exclusive access to the entire range (Brown 1963). This portion of the feeding range can be called the area of local dominance (Kaufmann 1983; Maher & Lott 1995).

We propose, for the first time to our knowledge, that individuals holding adjacent areas of local dominance can establish beneficial interactions within feeding aggregations, similar to those occurring between adjacent neighbours in species that do not aggregate to feed. In the case of neighbouring territory holders, adjacent neighbours often tolerate each other reciprocally (the 'dear

enemy effect', Temeles 1994) and obtain a benefit by reducing the energy they would otherwise invest defending shared territorial boundaries (Godard 1993; Hyman 2002; Krams *et al.* 2008). In the case of species that aggregate to feed, we propose that reciprocal tolerance between individuals that hold neighbouring areas of local dominance ('adjacent neighbours') can reduce competitive interference at aggregations and increase food intake. Tolerance of adjacent neighbours would be regularly reciprocated if aggregations occurred in the dominance area of each adjacent neighbour with similar probability, which is feasible in the many species that congregate at unpredictable food patches (Krause & Ruxton 2002).

We tested the 'reciprocal tolerance' hypothesis in the ocellated antbird (*Phaenostictus mcleannani*), a neotropical bird that follows diurnal swarms of nomadic army ants to capture arthropods fleeing from the ants. Ocellated antbirds live in stable mated pairs for several years, and pairs usually feed together; offspring roost and feed with their parents for at least five months. Each pair holds a large (50 ha) stable feeding range, but roosts and nests in a smaller area (6 ha) located in the core of the feeding range. The roosting area of each pair is surrounded, on average, by the roosting areas of four adjacent neighbouring pairs (range 2–6; J. Chaves-Campos 2007, unpublished data). Neighbours and non-neighbours aggregate daily at swarms and aggregations disband daily (Willis 1973; Chaves-Campos & DeWoody 2008). Ocellated antbirds (both sexes) vocalize loudly while feeding to answer the 'loud songs' of other individuals (Willis 1973), and antagonism at swarms can escalate until one individual chases the other (J. Chaves-Campos 2007, personal observation). Individuals significantly differ in the pitch of their songs

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(Y. Araya-Ajoy & J. Chaves-Campos 2007, unpublished data), which suggest that ocellated antbirds could distinguish adjacent neighbours from others by their songs.

In the related bicoloured antbird, the male whose nest is closest to the swarm displaces other individuals (except his mate and young offspring) from any perch he chooses at the front of the swarm, where prey are densest (Willis 1967). Ocellated antbirds also compete for access to perches at swarm fronts (Willis 1973), and because they nest in their roosting areas (Chaves-Campos & DeWoody 2008), we asked whether an individual would be dominant over others in this area. We tested this idea using simulated acoustic aggressive challenges at different distances from the centre of the roosting area of each bird, and we asked whether responses were less aggressive when the challenger was an adjacent neighbour, as our reciprocal tolerance hypothesis predicts. We also recorded perch displacements at swarm fronts to test the additional prediction that displacements would be biased towards non-adjacent neighbours. Finally, we tested whether prey intake was higher in an individual's roosting area and in the roosting areas of adjacent neighbours compared with feeding in more distant areas.

2. MATERIAL AND METHODS

(a) Study site and general protocols

We studied ocellated antbirds in 392 ha at La Selva Biological Station (10°25' N, 84°01' W), Costa Rica, where they follow only the army ant *Eciton burchellii* (Chaves-Campos & DeWoody 2008). We banded and molecularly sexed 75 individuals (adults and juveniles from at least 21 mated pairs) between June 2004 and December 2007 (88% or more of the adults roosting in the study area, Chaves-Campos & DeWoody 2008). Thirty-four birds (17 males and 17 females) from 17 pairs were radiotagged to determine ranging patterns and interindividual interactions. Observations and experiments were conducted in all months to prevent seasonal bias, although the effect of seasonality might be unimportant because ocellated antbirds breed year-round (Willis 1973). We assessed the effect of breeding condition when possible.

We used 10 or more different locations per tagged individual (average 25) to define roost centres and roosting areas. Roost centres were calculated with the program WEIGHTED MEAN OF POINTS (Jenness 2004), and roosting areas were delineated with the kernel method as in Chaves-Campos & DeWoody (2008). The overlap between the roosting area of a pair with those of adjacent neighbours was small (mean $\pm$ s.d. = $9 \pm 4\%$; J. Chaves-Campos 2007, unpublished data), suggesting possible local dominance. Roosting area boundaries might not perfectly reflect diurnal local dominance, and for this reason, we did not collect foraging and interaction data in overlapping zones to minimize the risk of misassigning individuals to roosting areas.

(b) Feeding location

Feeding locations were only recorded from the first swarm where each individual was found in the morning (birds stayed at the first swarm until the afternoon on 88% of days; J. Chaves-Campos 2007, unpublished data), at least three times a week for each individual. We examined the distribution of feeding locations by distance from the roosting area of the focal individual (in its own roosting area, in the

roosting area of an adjacent neighbour, next-adjacent neighbour, neighbour removed two ranges or more distant locations) using repeated-measures analysis of variance (see electronic supplementary material for details). We included sex as a fixed effect (categorical; as in all subsequent analyses) to evaluate sex differences.

We also used Kolmogorov–Smirnov (KS) tests to compare the total observed frequency distribution of feeding locations by distance from the roost centre with a hypothetical distribution based on (i) the area and (ii) the number of roosting areas expected for each distance (categorized as above). See electronic supplementary material for calculations. Both yielded similar results, and only the latter is shown.

(c) Prey intake

Prey intake was sampled from a blind less than or equal to 5 m from birds feeding at swarms (birds fed readily near the blind). The number of arthropods eaten by a focal bird was counted using binoculars for 5–15 min before switching to another individual. Focal birds were opportunistically chosen to sample prey intake in different roosting areas. Prey length was estimated in relation to the exposed part of the bill in three categories: small (1 bill=18 mm long, Willis 1973), medium (1.5 bills) and large (2 bills). The number of prey eaten was standardized to bill-size units and expressed as a rate (prey min⁻¹).

Weather conditions affect *E. burchellii* activity (O'Donnell *et al.* 2007) and were measured during each sampling period by an automatic meteorological station (ambient temperature, precipitation and humidity). The activity of *E. burchellii* swarms declines in the afternoon at La Selva (O'Donnell *et al.* 2007), so we collected nearly all samples before noon and recorded the hour in which each observation was made. The size (width) of the swarm can affect prey intake through competition (Willson 2004) and was visually estimated from the blind (to prevent disturbance) to the closest metre at the end of each observation period. The maximum number of conspecifics and heterospecific birds observed around the focal bird during each observation period was recorded. We regarded these numbers as reasonably accurate estimates of the number of potential competitors for the focal bird. All observations were recorded with a digital voice recorder.

We analysed prey intake rates according to the location of the swarm in relation to the roosting area of the focal bird: in its own, in the roosting area of an adjacent neighbour, next-adjacent neighbour or more distant locations (separated by ≥ 2 ranges) and locations deep into secondary forest where no birds roosted (figure S1, electronic supplementary material). We used analysis of covariance (ANCOVA) to account for all measured cofactors, which were included individually in the model. Weather variables were an exception because they were summarized using principal component analysis (PCA) owing to sample size limitations (tables S1 and S2, electronic supplementary material).

To place intake rate differences in perspective, we used the correlation between insect size and biomass (Rogers *et al.* 1976; Stork & Blackburn 1993) and the correlation between avian field metabolic rate and body size (Nagy 2005) to estimate the number of prey an average-sized ocellated antbird (50 g, Willis 1973) needs to consume to meet daily metabolic requirements.

(d) Displacements

Displacements occurred when a bird moved to another perch immediately following the approach of another bird that then occupied the original perch of the departed bird. Dyadic displacements from perches at swarm fronts were recorded simultaneously with prey intake. We used a resampling method to test the prediction that displacements were significantly biased towards non-adjacent neighbours (i.e. a one-tailed test). We constructed a random distribution of dyadic displacements across ant swarms and compared it with the total observed number of displacements across swarms. The distribution was constructed by randomly sampling dyads from each swarm to create random dyadic displacements. The number of swarms, the number of dyadic displacements in each swarm and the number of adjacent and non-adjacent neighbour dyads that were available in each swarm were as observed. We added the number of random dyadic displacements between non-adjacent neighbours across all swarms to generate a total random value. The procedure was repeated 1000 times to generate the distribution.

(e) Dominance areas and recognition of adjacent neighbours

We tested for site specificity of aggression with simulated acoustic challenges at ant swarms located at different distances from the roost centres of radiotagged birds. We used loud songs of adjacent neighbours or non-neighbours (individuals that roosted three or more roosting areas away from the radiotagged birds present at the swarm) as aggressive stimuli. Songs from six adult individuals recorded from La Selva and two from the adjacent Braulio Carrillo National Park (roughly 10 km away) were used in the experiments. Songs from La Selva were from four males and one female, and the other songs were from birds of unknown sex. The sex of the stimulus source did not affect the outcome, in that results were unchanged when the analysis included only stimuli from known males (figure S2, electronic supplementary material). Songs were recorded 10–20 m away from singing individuals using a Sennheiser ME 66 microphone attached to a Sony minidisk recorder. Songs were digitized with no compression at a sampling rate of 44.1 kHz and standardized in the program RAVEN 1.3 to approximate the sound pressure level of field records (60 dB at 10 m, measured with a Sper Scientific 840014 mini sound meter).

We broadcast the stimulus at opportunistically chosen swarms, exposing all radiotagged individuals present to the same stimulus. Each radiotagged bird was exposed to an adjacent-neighbour and to a non-adjacent-neighbour stimulus on different days, usually at more than two different distances from their roost centre: less than or equal to 250 m and greater than 250 m (the roost centres of adjacent neighbours are separated by an average of 250 m, Chaves-Campos & DeWoody 2008). We never exposed an individual (known by radio signal) to its own song, and we performed not more than one trial on the same individual per day to limit possible carry-over effects between responses (Podos 2007). We rotated the recordings used in the playback experiments among trials and did not broadcast the same stimulus more than once to the same bird to minimize pseudoreplication (Kroodsmas 1990).

The stimulus consisted of three 1 min periods of 'loud' songs separated by 1 min of silence, for a total of 5 min of

playback, and was broadcast 20–30 m away from the swarm from a Polyplanar MA840 speaker (frequency range: 70 Hz to 14 kHz) connected to a digital CD player located 10–20 m from the speaker. One researcher (concealed in a blind) broadcast the stimulus and recorded the response (i.e. radiotagged bird(s) travelled from the swarm to the speaker and sang loud songs) or lack thereof of each individual present during a 10 min period after the stimulus ended or after a bird started singing, whichever came first. Acoustic responses were recorded using the equipment described earlier. A second researcher, concealed in another blind 10 m behind the speaker, identified the responding bird(s) with binoculars and/or by detecting a strong increase in its radio signal (all responding individuals were radiotagged and/or banded).

We evaluated whether the individuals present at swarms responded to challenges near the centre of their roosting areas by modelling the probability of responding (yes, no) as a function of the distance from the swarm to the roost centre of each individual present, using logistic regression (binary error structure). Distances were calculated in the program ANIMAL MOVEMENT 2.04 (Hooge & Eichenlaub 1997). The number of individuals present and the acoustic stimulus (adjacent neighbour and non-neighbour) were included as cofactors. We quantified the intensity of vocal responses by measuring latency to singing, total number of loud songs and time spent singing during the response. These variables were summarized using PCA, and the first PC, which explained most of the variation in response intensity (table S3, electronic supplementary material), was used as response variable in an ANCOVA that included the type of stimulus (adjacent neighbour and non-neighbour) as a factor and the distance from swarm to roost centre as a cofactor.

3. RESULTS**(a) Feeding location**

We recorded 1346 feeding locations from 31 individuals (16 females and 15 males) that were observed 15 or more times. Sex did not affect the distribution of observations ($F_{1,69} = 0.05$, $p = 0.83$). Feeding locations by individual were not equally distributed in space ($F_{4,113} = 37.8$, $p < 0.001$). Individuals fed in their own roosting area during 5 per cent of the observations, in the roosting area of an adjacent neighbour during 35 per cent of the observations and at more distant locations the rest of the time. The total frequency distribution of feeding locations was very similar to the distribution per individual (figure 1). The proportion of total feeding locations was higher than expected within two roosting areas from a given roost centre and lower than expected beyond that distance (KS, $D_{\max} = 0.39$, $p < 0.001$). The distribution of observations was similar for individuals with confirmed breeding status (figure S3, electronic supplementary material).

(b) Prey intake

We recorded the number and size of prey eaten by individuals in 141 feeding bouts (16 birds; 11 males and 5 females from 10 different pairs). All feeding observations were made at swarm fronts. In only seven observations were birds feeding in their own roosting area (in agreement with figure 1); 15 were in the roosting areas of an

Figure 1. Army ant swarms visited by distance from the roost centre of focal ocellated antbirds (in roosting area units; one roosting area = 250 m in diameter). Swarms were found in the roosting areas of the focal individual (own), adjacent neighbours, next-adjacent neighbours (1), neighbours removed 2 ranges (2) or more distant locations (>2). White bars, average $\pm$ s.e. across individuals; grey bars, total observed distribution; black bars, total expected distribution according to the area encompassed by each distance. Different letters denote significant differences between means.

adjacent neighbour, 58 in the roosting area of a next-adjacent neighbour and 61 at more distant locations. We found no significant difference between prey intake rates in the roosting areas of focal birds (0.30 ± 0.09 prey min^{-1}) compared with the roosting areas of adjacent neighbours (0.27 ± 0.04). Both were higher than feeding rates in more distant locations ($0.15 - 0.19 \pm 0.03$). The small sample size from the 'own' category resulted in large standard errors that made *post hoc* analysis difficult to interpret. We therefore pooled the own and adjacent neighbour categories and performed the analysis again.

All cofactors affected prey intake, except for the number of conspecifics ($F_{2,12} = 1.2$, $p = 0.33$) and hour ($F_{5,24} = 1.9$, $p = 0.13$) (table S2, electronic supplementary material). Males obtained slightly higher intake rates than females but only during rainy weather ($F_{1,114} = 7.9$, $p < 0.01$; figure S4, electronic supplementary material). After controlling for the effect of cofactors, intake rates were 60 per cent higher in the roosting area of an adjacent neighbour or closer compared with more distant locations for all prey sizes, either separately or combined (for combined: $F_{2,13} = 4.4$, $p = 0.03$). Given mean daily intake rates (figure 2), it should take an ocellated antbird 180 min of continuous feeding in its own or in an adjacent neighbour's roosting area to meet daily minimum metabolic requirements (about 50 bill-size prey items). It should take approximately twice as long (300–360 min) to meet requirements in more distant locations.

(c) Displacements

We recorded 30 cases in which one bird displaced another from a perch at the front of the swarm (1434 min of observation; 44 different swarms). Displaced individuals remained at the front, but they were forced to move to

Figure 2. Mean feeding rates of individual ocellated antbirds in the roosting area of: own+adjacent neighbour, next-adjacent or more distant locations. Means and s.e. were adjusted by the effect of significant cofactors (least-square means). Different letters denote significant differences between means.

another perch. We were able to identify both dyad members on 11 occasions (involving 11 different individuals), and all of these displacements occurred between non-adjacent neighbours. This is higher than expected by chance ($p = 0.049$; table S4, electronic supplementary material), which suggests that displacements were biased towards distant neighbours. In six cases, a male displaced a female, whereas in the other five, one male displaced another male, which suggests that males displace conspecifics more often than females even after taking into account a 2:1 male:female ratio at these swarm fronts ($\chi^2 = 8.8$, d.f. = 3, $p = 0.03$).

(d) Dominance areas and adjacent neighbour recognition

We conducted a total of 40 acoustic challenges at swarms. Three radiotagged birds were present on average for each challenge, including a total of 14 radiotagged birds (nine adult males, one juvenile male and four adult females). In each case, a responding bird was recorded in addition to a list of non-responding individuals. The responding individual left the swarm and circled the speaker while singing loud songs and showing aggressive postures (*sensu* Willis 1973), which allowed us to confirm visually that only one individual responded in each case. Only one adult radiotagged male responded vocally in each trial, despite the presence of other adult males, juveniles and females. There were two exceptions: an adult male and its juvenile son responded together and an adult female responded in the only case in which no males were present.

The probability of responding decreased as the distance from swarm to roost centre increased ($F_{1,37} = 4.72$, $p = 0.04$) and was also affected by the presence of additional adult males ($F_{1,37} = 6.26$, $p = 0.02$) (figure S5, electronic supplementary material). The responding individual was always the closest to its roost centre among potential respondents. The six birds tested in their roosting areas (less than 250 m from their roost centre) responded vocally despite the presence of other males. Only 14 of the 34 birds tested greater than or

equal to 250 m from their roost centre (i.e. outside their roosting areas) responded vocally. Of these 14 responses, 11 occurred when no other male was present and three occurred in the presence of an adjacent male neighbour, but outside the roosting area of both males. The probability of responding was similar for the adjacent neighbour and non-neighbour stimuli ($F_{1,6} = 0.22$, $p = 0.66$).

Although the probability of responding was similar for the adjacent-neighbour and non-neighbour stimuli, vocal response intensity varied between stimuli. We quantified response intensity in 16 instances from eight individuals. The birds responded less aggressively to adjacent neighbours than to non-neighbours ($F_{1,5} = 35.6$, $p = 0.002$) after controlling for the distance from swarm to roost centre ($F_{1,6} = 8.8$, $p = 0.025$). Least-square mean intensity scores (in PC1 units) were -2.3 ± 0.4 (s.e.) for adjacent neighbours and 1.3 ± 0.3 for non-neighbours. Responses to non-neighbours included more loud songs (19 ± 4 versus 13 ± 2) and were usually longer in duration (222 ± 40 versus 180 ± 50 s) but similar in latency (117 ± 34 versus 102 ± 19 s).

4. DISCUSSION

(a) *Local dominance*

The results from the playback experiment suggest that night-time roosting areas correspond to areas of diurnal dominance, at least in the sense of eliciting aggression when individuals are challenged near their roost centres. Ocellated antbird males responded to aggressive challenges in their roosting areas, regardless of the presence of other males but did not respond outside this area unless no other males were present. This suggests that exclusivity of roosting areas is based on diurnal site-dependent dominance, and that the presence of other males inhibits aggression outside a male's roosting area. The general lack of responses from juveniles and females, and the lack of displacements of males by females, suggests that adult males are dominant in this context, as previously suggested (Willis 1973).

(b) *Reciprocal tolerance*

Despite small samples for some analyses, the data are consistent with the hypothesis of tolerance of adjacent neighbours in feeding aggregations. Males responded less intensely to vocalizations of adjacent neighbours than to those of non-neighbours, suggesting tolerance of the former (i.e. 'dear enemy' effect). Reduced vocal aggression to adjacent neighbours is consistent with the result that displacements at swarm fronts were biased towards non-adjacent neighbours. Our interpretation is that when ocellated antbirds aggregate to feed in the roosting area of a given male, this male is more tolerant to adjacent neighbours than to distant neighbours (regardless of their sex) at the front of the ant swarm, resulting in a reduction in competition for food between adjacent neighbours. Females and offspring usually feed next to their mate and father, respectively (Willis 1973), suggesting that they benefit from male dominance. This is consistent with the increase in prey intake recorded for individuals (regardless of sex) in their own roosting areas and in the roosting areas of adjacent neighbours compared with more distant locations.

The decrease in intake rates for an individual feeding in the roosting area of a distant neighbour could be caused by displacement from the swarm front or by a decrease in foraging efficiency owing to an increase in actual or potential intraspecific aggression. The fact that all individuals were observed feeding at swarm fronts is consistent with the latter. We did not detect a decrease in prey intake related to the number of conspecifics present at the swarm, but the decrease in prey intake beyond the roosting areas of adjacent neighbours suggests possible costs of feeding in those areas. Costs of tolerance may not be balanced by benefits to kin since most (i.e. 80%) male adjacent neighbours are unrelated (Chaves-Campos & DeWoody 2008).

The fact that intake rates were low in secondary forest (included in the distant location category), where dominance areas were absent (figure S1, electronic supplementary material), deserves an explanation. Intake rates were expected to be higher in secondary forests because of the absence of locally dominant conspecifics, but it is possible that the decrease in prey intake in secondary forest is due to elevated heterospecific competition. The biomass of heterospecific competitors in secondary forest is three times higher than the old-growth forest (C. A. Lizana-Moreno & J. Chaves-Campos 2007, unpublished data).

One potential explanation for why only adjacent neighbours show reciprocal tolerance at swarms is that this tolerance is developed in the process of establishing adjacent roosting areas and remains stable over time, as in many strictly territorial species that show the dear enemy effect (Ridley *et al.* 2005). In addition, the probability of reciprocal tolerance can depend on the frequency with which individuals meet (Krams *et al.* 2008), which should be higher for birds that hold adjacent dominance areas. Tolerance of adjacent neighbours could be reciprocated on a regular basis because swarms of *E. burchellii* very probably occur in the roosting areas of each individual with similar probability because of the unpredictable wide-ranging movements of the ants (Franks & Fletcher 1983).

(c) *Implications for obligate ant-following behaviour*

About 50 species of birds from different families are known to feed regularly at army ant swarms (Willis & Oniki 1978). The similarities in territoriality and foraging behaviour between ocellated antbirds and other army-ant-following birds (Willis 1967, 1972; Willson 2004) suggest that the theory of reciprocal tolerance presented here could be applicable to those species. Reciprocal tolerance could have also been a necessary condition in the evolution of obligate army-ant-following behaviour, at least in antbirds. Obligate ant following has evolved in only a few species of antbirds, and their ancestors probably fed at swarms opportunistically in their defended territories (Brumfield *et al.* 2007). Species that evolved obligate ant-following behaviour probably relaxed strict territorial defence to follow nomadic army ants beyond territory boundaries, but also retained local dominance to ensure high feeding rates, which can be critical during the breeding season and/or during rainy periods

because rain halts swarming in *E. burchellii* (Willis 1967; Teles da Silva 1977). We offer a first approximation of the magnitude of the advantage conferred by local dominance and reciprocal tolerance. Individuals fed in their roosting areas in 5 per cent of the observations (figure 1) and showed a 60 per cent increase in prey intake in those areas compared with more distant locations. This increase would result in an overall gain of 3 per cent over time compared with a scenario without local dominance (intake rates assumed to be similar for all individuals outside their roosting areas). Birds fed in the roosting areas of adjacent neighbours in 35 per cent of the observations, so that tolerance by adjacent neighbours increases prey intake by 60 per cent over 35 per cent of their feeding bouts for an overall increase of 20 per cent over time, compared with the previous scenario of only local dominance.

(d) Implications for other taxa

Many vertebrates feed in aggregations (Krause & Ruxton 2002) and some show local dominance (Oberski & Wilson 1991; Maher & Lott 1995; Waterman 2007; Krams *et al.* 2008); however, very little is known about the occurrence of reciprocal tolerance in species that form aggregations (Müller & Manser 2007; but see Radford 2005; Boesch *et al.* 2008). The ocellated antbird system offers a starting point to identify factors that favour tolerance of neighbours in species that aggregate to feed. In this system, high intraspecific competition for food is probably a major factor favouring dominance areas to ensure access to food in the core of an individual's range, and tolerance of adjacent neighbours can further increase prey intake in an environment with a low probability of finding enough swarms in a relatively small dominance area. By contrast, low intraspecific competition for resources seems to favour tolerance of neighbours in species that defend territorial boundaries, whereas strong competition causes aggression towards neighbours (Müller & Manser 2007).

Social territorial species can defend an area that reliably provides sufficient resources, with no need for movement across the range of others. By contrast, ocellated antbirds must track a concentrated but shifting food supply, and movement over a large range is facilitated by local dominance tempered by tolerance among neighbours. Shifting resources that reliably renew appear to favour this flexible system that combines a core of competitive advantage with a larger range in which competitive interference increases with distance from the core.

This research followed ethical guidelines set by the Purdue University Animal Care and Use Committee.

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