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Tracking the warriors and spectators of acorn woodpecker wars

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Although intergroup conflict is widespread in vertebrates, simultaneous agonistic interactions among several groups are rare [1]. Acorn woodpeckers (*Melanerpes formicivorus*) are cooperatively breeding birds that defend acorn storage facilities ('granaries'), which provide significant survival and reproductive benefits to breeders in the social group [2]. Breeder vacancies in high-quality territories (*i.e.*, large granaries accrued over multiple generations) elicit violent fights or 'power struggles', among multiple same-sex coalitions from neighboring groups. Here, using an automated radio-telemetry system, we found that individuals in coalitions competing for breeding vacancies — the 'warriors' — invested up to ten hours per day on successive days before one coalition emerged victorious. Power struggles also attracted 'spectators'— acorn woodpeckers not eligible to fill the breeding vacancy. Apparently present only to gain social information, spectators travelled from territories as far as over three kilometers away. Our study reveals the complexity of acorn woodpecker social group networks, demonstrating the significant effort of both warriors and spectators to pursue fitness benefits and obtain social information.

Acorn woodpecker groups live on year-round territories defined by granaries, trees with hundreds to thousands of holes, drilled by the birds, where they store acorns for later consumption (Figure 1A). Stored acorns are consumed by adults when food is scarce and are also fed to nestlings. Granaries are pilfered by intra- and interspecific competitors and are thus zealously defended by all group members. Large-granary territories are often controlled by polygynandrous groups consisting of multiple male and female breeders and their non-breeding offspring ('helpers'). Same-sex co-breeders are closely related to each other but unrelated to breeders of the opposite sex [3]. In addition to within-group dynamics, acorn woodpeckers recognize associations among individuals outside their group and track membership changes in surrounding territories [4]. This information transfer is likely to occur via numerous daily off-territory forays to neighboring territories [5].

A typical way that non-breeding helpers obtain a breeding position is by filling a breeder vacancy in a non-natal territory. In our California study population, same-sex coalitions of

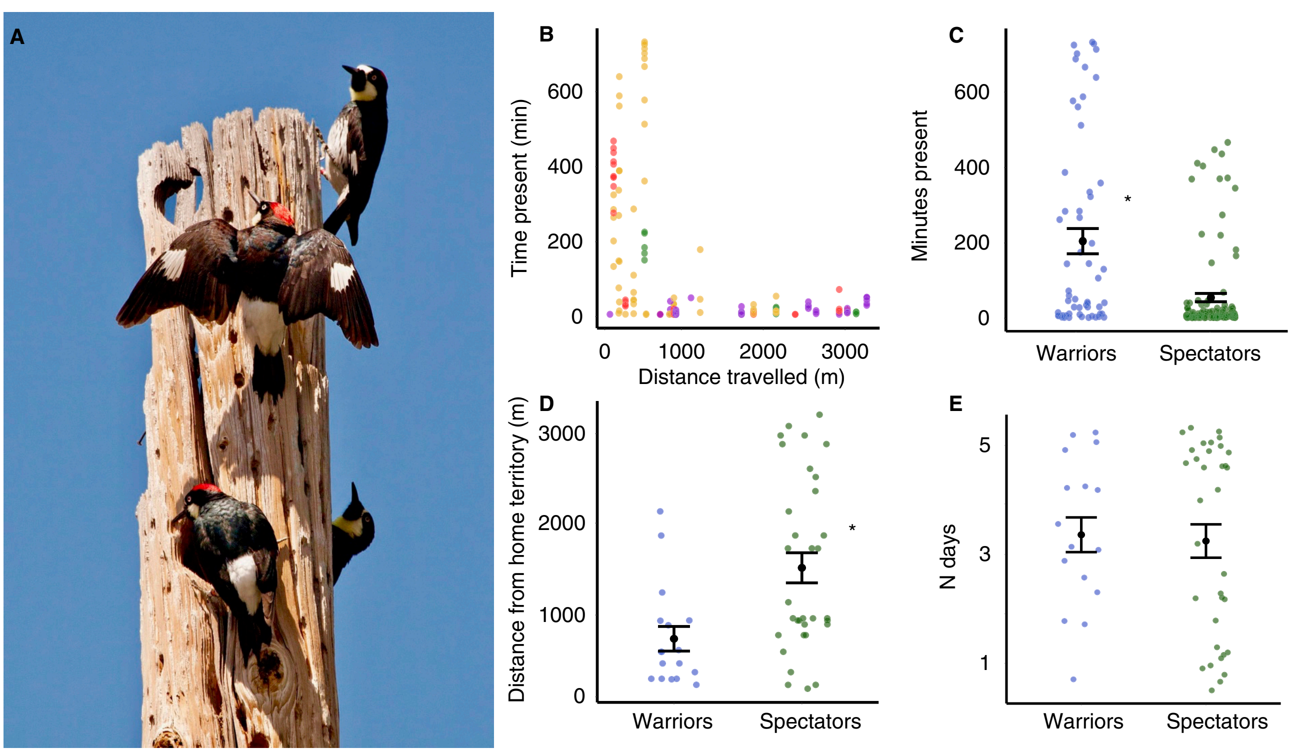

Figure 1. Acorn woodpecker behavior at power struggles.
(A) 'Spread-wing' display by a female acorn woodpecker on a granary (photo: © Bruce Lyon). (B–E) Variation in individual investment in power struggles. Black points represent the mean for each variable; error bars denote standard errors. Asterisks indicate statistically significant differences. (B) Birds from >3 km away visited power struggle sites. Colored points indicate time spent (min) attending power struggles by each sex-status category as a function of distance to home territory for warriors (yellow = helper females), and spectators (purple = breeder females, green = breeder males, red = helper males). (C) Helper female warriors spent significantly longer times ($P < 0.05$) at power struggles compared to spectators (birds present but not competing). (D) Warriors attending power struggles came from groups significantly closer than spectators. (E) There was no difference ($P > 0.05$) in the duration of attendance (days) by individual warriors and spectators at a power struggle.

helpers will fight against a dozen or more competing coalitions (40 or more birds) for a breeding vacancy, with winners co-breeding at the new territory [6]. Typically, a quarter of the about 50 groups we follow have a breeding vacancy in a given year; although long, violent power struggles that attract a large number of birds tend to happen at territories with big granaries [7]. Such power struggles can last for several days and involve spread-wing displays (Figure 1A), incessant calling, and intense physical — sometimes fatal — fights [6]. A key to understanding the factors driving the success of a coalition in achieving breeding status involves quantifying the effort expended by coalition members that travel to, and fight at, power struggles. However, visually monitoring behavior at power struggles — especially individual investment — is difficult due to the chaotic nature of these conflicts.

Using an automated radio-telemetry system [5], we tracked 36 acorn woodpeckers that attended three power struggles (2018: May, Aug.; 2019: Apr.). Because each power struggle was triggered by a female breeder vacancy, we expected helper females to invest the most effort as warriors [6,7]. Females with a breeding position at another group, as well as any males, were considered spectators, since such individuals were not relevant to the female vacancy. Although not the case with tagged birds in this study, it is possible that such individuals were assisting helper coalitions from their home groups (their own offspring). Given the tradeoff between gaining information at a power struggle *vs*. defending a home territory [5], we did not expect to detect many spectators at power struggles. We used linear mixed models (Supplemental information) to test whether a bird's role as a warrior or spectator explained variation in time spent at power struggles (*i.e*., number of minutes a tag was detected by a receiver at the granary), and distance traveled to reach power struggles from home territories.

The three power struggles attracted about a third (31 ± 7%) of all radio-tagged birds in our study area (N = 41/61/73) at the time of each event. Some birds visited power struggles from over three kilometers away, close to the maximum distance between any two groups in our study area (Figure 1B). As expected, warriors spent the most time at the power struggles: helper females (total N = 13) attended power struggles for nearly 113 minutes longer per day (mean ± SE 112.8 ± 28.5 min) than spectators (N = 23, $P < 0.001$, Figure 1C). During one power struggle, two helper female coalition members returned over four consecutive days, staying over ten hours each day (Figure 1C), but did not win the power struggle; an untagged female coalition ultimately won the breeding position. Such a continuous presence at these conflicts demonstrates a remarkable willingness to expend intense short-term effort for potential access to the long-term benefits of a breeding position at a high-quality territory.

Spectators spent almost an hour per day attending power struggles (mean ± SE = 52.1 ± 10.4 min/day, range 1–462 min; Figure 1B,D). This suggests that maintaining current information within the acorn woodpecker social network is worth leaving a home territory unattended for considerable periods of time. Warriors came from group territories that were significantly closer (mean ± SE = 644 ± 136 m) than spectators (1432 ± 167 m) ($P < 0.001$, Figure 1D). Additionally, there was no difference in the number of days warriors and spectators visited any one power struggle site ($P > 0.05$, Figure 1E). Spectators are thus clearly willing to repeatedly travel considerable distances, apparently even farther than those competing for the vacancy, to gather social information.

Our study not only demonstrates the significant effort invested by some individuals to ensure long-term fitness benefits, but also reveals that social birds — including those that already have a breeding position — foray well beyond their home territory to gather social information [8]. Automated radio-telemetry is thus a powerful tool that can help reveal individual investment in complex social behaviors like power struggles; future studies should link such social events to the flow of information through social networks [9,10].

SUPPLEMENTAL INFORMATION

Supplemental Information includes one figure and experimental procedures and can be found with this article online at https://doi.org/10.1016/j.cub.2020.07.073.

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SUPPLEMENTAL INFORMATION

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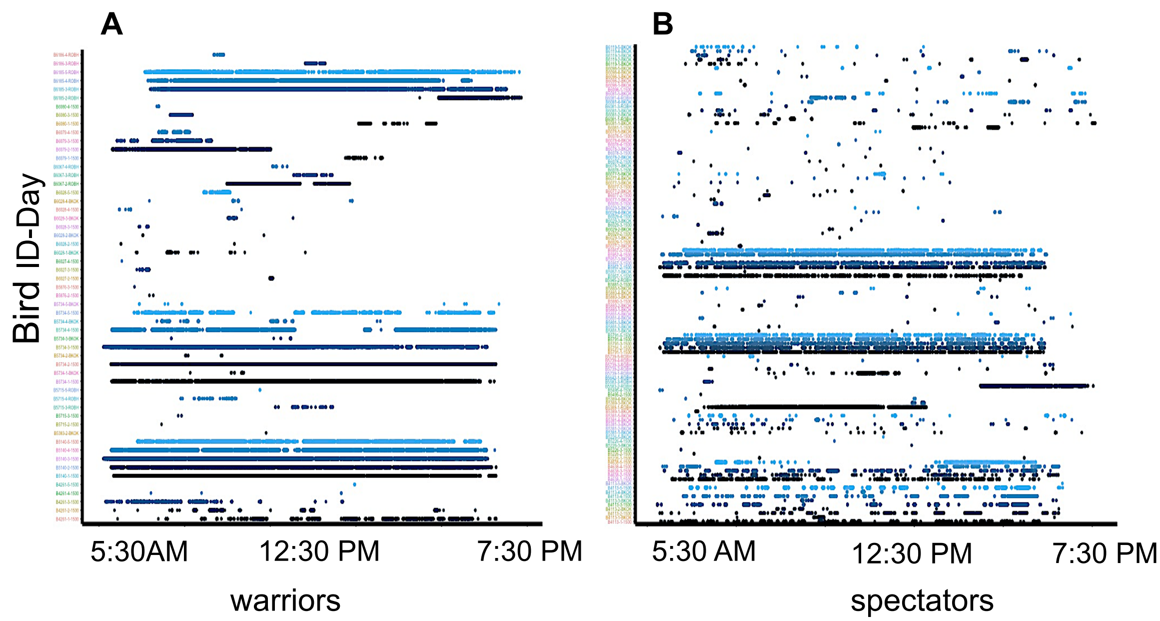

Figure S1: Variation in distribution of acorn woodpecker detections at power struggles. Detections depicting time spent at power struggle sites by A) warriors (N=13) and B) spectators (N=23) throughout the day. Individual birds are denoted by unique font color in the Y-axis. Each point represents a detection of the bird on a given day in the power struggle. The relative shading of the point represents the day in the power struggle. Day-1 is darkest and Day-5 has the lightest shade. Data includes detections from all three power struggles.

SUPPLEMENTAL EXPERIMENTAL PROCEDURES

Author contributions

S.B. conducted the fieldwork, analyzed data, and wrote and edited the manuscript, A.S.L. and R.M.B. analyzed the data, and wrote and edited the manuscript. W.D.K. and E.L.W. raised funding for the study, conducted fieldwork, and edited the manuscript.

Study area and study species biology

We studied acorn woodpeckers at Hastings Natural History Reservation (36.387° N, 121.551° W) in central coastal California, USA. Adults on their natal territory with their social (and genetic) parents were categorized as nonbreeding helpers. Group members living outside their natal territories, or living with birds of the opposite sex that were nonrelatives, were considered putative breeders [S1]. Extra-group mating, as well as incestuous mating, is rare in our study population [S1, S2]. From 1973 to 2019, the majority of the woodpecker population was color-banded (N = 6184 total individuals) and monitored continuously for group size and composition. Each year, territory quality was assigned to each acorn woodpecker social group based on the size of the group's granary (1: <1000 storage holes [low quality], 2: 1000–2500 [medium quality], 3: >2500 [high quality]) [S3]. All power struggles in this study took place at high-quality sites.

Automated telemetry system

Acorn woodpeckers were caught opportunistically and fitted with dorsally mounted solar-powered nanotags [S4] with leg loop harnesses adjusted for body size [S5]. All tags weighed less than 1% of each bird's body mass. Radio-tagged birds were detected at power struggles by permanently installed autonomous, solar-powered base stations during daylight hours [S6]. The base stations installed near the granaries where the power struggles occurred were part of a larger array of 43 base stations throughout the research site.

Tags produced an encoded 64-bit, 2.5 ms radio ping every 1.5 s during the day, even in cloudy weather. Each detection of an individual at the base station was accompanied with a date, time, and signal-strength stamp. All detections were stored in files created every 15 min and stored on removable memory drives. Because the date a power struggle was initiated (i.e., after the death or disappearance of all breeders of a particular sex) is difficult to determine, we analyzed data from receiving stations at the sites 2 days before and after the peak of the power struggle, denoted by the day when the largest number of tagged birds were detected by the receiving station.

Time spent at the power struggle

We partitioned the time between 0600 and 2000 hrs (i.e., the widest potential window of woodpecker activity during the study period) into 1-min intervals. A bird was considered present at the power struggle site if the base station associated with that territory had the highest signal strength among the array during any particular 1-min interval. Our signal strength-cutoff, based on previous validation, indicated when the bird was within 100 m of the base station.

We further tested the accuracy of our location assignment as follows. For each five-day power struggle period and the individuals included in our analysis, we tested whether any bird detected at any base station in our 43-base station array was also detected at any other base station(s) with high signal strength during the same 1-min interval. During one power struggle period, 93.5% of all detections were at a single base station in any given minute, while 6.5% of the detections were at two base stations. For the other two power struggle periods, 100% of all birds were detected at only one base station within any 1-min interval. The next closest base stations to all three power struggle sites were more than 150 m away. These data suggest that our location assignments for birds were correct and largely safe from false positives. We calculated total time spent at the power struggle as the sum of all the 1-min intervals when a bird was present at the power struggle. The distribution of raw detections throughout the day are shown in Figure S1.

Statistical analyses

To test the proportion of tagged birds detected at the power struggle, we calculated the ratio between the number of birds detected at the power struggle site base station and the number of tagged birds detected in our entire 43-base station array during the power struggle. We tested whether helper females that were competing for the breeding position at power struggles – the warriors– spent more time at power struggles and came from groups farther away than the males of both status categories and breeder females – the spectators – in the population using the ‘Time spent at power struggle metric’ described above. For these analyses, we examined whether a) bird category (warrior or spectator), and b) distance from home territory was a significant predictor of minutes spent per day at the power struggle; we used linear mixed models with the power struggle group identity as a random factor (since some individuals were detected at more than one power struggle). We then used the number of days a bird was detected at each of the power struggle sites to test whether helper females (warriors) visited power struggles more than other sex-status categories (spectators).

All analyses were conducted in R 3.6.3 [S7]. We used the packages *lme4* [S8] and *lmerTest* [S9] for model building and evaluation. We report relative differences in metrics as calculated from linear mixed model estimates to facilitate interpretation of our results. The *P*-values reported for all mixed models were obtained from the output in the package *lmerTest*. Figures, however, were plotted with raw means and standard errors.

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