Social and Foraging Behavior in Northwestern Crows (*Corvus caurinus*): Incorporating New Analyses and Technology

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Abstract

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Both foraging and social decisions impact animals in important ways. We investigate the effects of age on foraging efficiency and sociality on Northwestern Crows (*Corvus caurinus*) at the beach, and use the growing field of social network analysis (SNA) to further examine social behavior in these birds. Specifically, we predict that 1) adults are more efficient foragers than juveniles, 2) juveniles interact with larger numbers of social partners than adults, 3) juveniles and adults prefer to associate with each other rather than within their own age classes, 4) crows are not associating randomly while on the beach (aka they have preferred social partners), and 5) pairs of individuals engaging in more affiliative behaviors with each other are less likely to also behave agonistically to one another, and vice versa. We also explore the uses of a remote radio detection system Encounternet by testing the validity of pilot data collected through this system against live observations conducted simultaneously. There is no effect of age on foraging efficiency; however, juveniles were found to interact with more total partners than adults, and most social associations occur between juveniles and adults. Our results also suggest crows are engaging in preferential social associations, though there is no evidence that affiliative pairs and agonistic pairs are mutually exclusive. Finally, it appears Encounternet can be useful for data collection when paired with live observations, as

long as certain limitations are kept in mind. Our pilot study could be beneficial to anyone considering the use of remote detection tools in data collection on animals.

Foraging behavior: Perhaps one of the biggest effects on an animal's fitness is its foraging efficiency (MacArthur & Pianka, 1966; Danchin, Giraldeau, & Cezilly, 2008). Individuals that cannot forage as well as others are at an obvious disadvantage in passing on their genes. Some more complex or demanding forms of foraging may need to be learned by youngsters before they are able to forage proficiently on their own. Northwestern Crows (*Corvus caurinus*) largely forage along the intertidal zone on beaches (O'Brien, Burger, & Dawson, 2005; Robinette & Ha, 2000), and typically fledge their young at 26-32 days of age (Butler, Verbeek, & Richardson, 1984). Prior to this, nestlings depend upon adults to provide their food, but after fledging are gradually weaned by adult crows. Many studies have been conducted on overall Northwestern Crow foraging efficiency (O'Brien, Burger, & Dawson, 2005; Richardson & Verbeek, 1986; Robinette & Ha, 1997), but to our knowledge none have tested whether this efficiency increases from juvenile to adulthood as young crows gain experience.

We compare the foraging efficiency (measured in average number of items per second of foraging) of juvenile and adult Northwestern Crows. We expect that adults will be more efficient foragers, reflected in a higher foraging rate than juveniles.

Social behavior: Sociality has always been a fundamental area of research in animal behavior and the driving force behind many of its classic studies (Trivers 1985, Wilson 1975). Aspects of social behavior include social foraging and kin selection, the idea that individuals should act more altruistically or cooperatively toward closer relatives due to a higher probability of said relatives sharing more of their own genes (Hamilton 1964, Smith 1964). Therefore we may expect, for example, to observe that animals prefer to associate more with kin than unrelated individuals or the background population as a whole.

Northwestern Crows (*Corvus caurinus)* are an excellent model for such studies as they live and forage in large fission-fusion groups, often gathering on beaches where opportunities for interactions with many potential partners abound (Robinette & Ha, 1997). They are monogamous and tend to be territorial off the beach, though slightly more gregarious than their cousins the American Crow (*Corvus brachyrhynchos*) (Madge & Burns, 1994). Because of their territoriality and wariness toward strangers, there is evidence that Northwestern Crows show signs of differential behavior towards kin and familiar individuals such as mates and offspring, vs. non-kin and strangers, suggesting a capacity for both kin and individual recognition (Ha, Bentzen, Marsh, & Ha, 2003). In addition, they have been observed preferentially associating with specific individuals at above chance levels while engaged in foraging, though the total number of such preferred social partners varies between individuals.

We predict that juvenile (first and second year) Northwestern Crows will associate with larger numbers of partners while foraging than adults, due to their dependence on their older family members. We further predict that, of the social associations we do observe on the beach, most will consist of adults and juveniles interacting with each other (heterophilic) rather than their own age-mates (homophilic), for the same reason as stated above.

One of the fast-growing areas of research in the field of sociality involves utilizing social network analysis (SNA) to quantify and track interactions and relations between animals. Social network theory is a sophisticated tool for the study of social behavior, which allows for quantification at the levels of both the individual and the population (Wasserman & Faust, 1994). Social networks consist of individuals (nodes) within a group or population and the interactions or ties between them, known as “edges.” These structures can provide graphical representations of the interactions between individuals that may not be as readily apparent by other methods. For example, “cliques”, or components consisting of select individuals that associate preferentially amongst each other above chance levels can be spotted more easily when displayed as part of a social network graph. Social network analysis also gives insights into the nature of interactions between individuals and/or groups. For instance, a network may be undirected, displaying overall trends of sociality among different nodes such as which individuals prefer to spend more time within a set distance of each other. A directed network, on the other hand, can track specific targeted behaviors (agonistic vs. affiliative, etc.) or the flow of information or disease between nodes. SNA may possess an added advantage over the simple social association methods mentioned above by allowing us to create networks of repeated interactions between specific individuals instead of the anonymous and less clear-cut dyads provided by association data.

Social network analysis (SNA) also possesses its own set of measurements to quantify the network. A node’s degree, for example, is determined by how many immediate partners it is connected to within the network, while its betweenness score is defined as how many paths between two other nodes pass through the focal node and therefore is a measure of connectedness. Using this information, we may be able to hypothesize, for instance, whether certain types of individuals are more likely to receive or initiate aggressive behaviors, or simply associate with larger numbers of partners in general (Wey, Blumstein, Shen, & Jordán, 2007). Despite its popularity among the social sciences for studying human behavior, SNA has only recently been applied to animal behavior (Krause, Croft, & James, 2007); but has the potential to transform the way we study sociality in the behavioral sciences.

One area in which SNA can be useful is studying the roles that individual animals play in socially complex foraging groups. By representing these foraging associations as social networks, we may be able to test whether certain crows (dominant vs. submissive, or adult vs. juvenile, for example) tend to have a higher number of partners, and by extension a higher degree of sociality in the population. This information would be useful in determining what factors affect sociality in the species, and by extension the quality of interactions between individuals, such as during foraging, and may be more repeatable than anonymous social associations.

We sought to confirm through novel SNA methods that crows on the beach are not associating at random; in other words, some birds possess a higher degree (number of foraging partners) than others, thus implying that some preferential assorting is occurring in a large group. We also refined our overall associations network by examining affiliative and agonistic behaviors in particular – we predicted that pairs or dyads of crows that regularly engage in aggressive encounters are less likely to also act cooperatively with each other. If this is true, we can further conclude that Northwestern Crows are capable of modifying their social behavior on an individual basis.

Another advancing area of animal behavior research is the utilization of remote and automatic detection technology that may aid in data collection, including social interactions. Such technology often involves specially-made radio tags that may be deployed on wild animals to record and log "encounters" between tagged individuals (known as "biologging", Rutz & Hays, 2009 or "radio frequency identification", Bonter & Bridge, 2011) and their surroundings. One of the obvious advantages of using radio tags for biologging is that it allows for continuous data collection as long as the tags are active, including during times and at locations that would not be feasible for personal observation. With the advent of tags possessing GPS logging capabilities, it is now even possible to pinpoint and track the locations and movements of wild animals, as well as their interactions with each other. While the first proximity loggers were bulky and large, over the last decade this technology has improved such that now tags can weigh as little as 1 g, making them appropriate for even small species (Krause, Wilson, & Croft, 2011). We collected data on Northwestern crows with a relatively new system, Encounternet (www.encounternet.com; Rutz et al. 2012), which consists of mutually-detecting radio tags and "base stations," receivers set up at various locations along the study site that are able to automatically download data from any tags within range.

A further advantage of many remote-detection systems in general, and Encounternet in particular, is their ability to obtain precisely time-stamped data. This feature is invaluable for data collection and analysis in which time of day or the date plays a large role, such as measuring tide height in terms of food availability, or breeding season. It can further allow us to measure how long individuals interact with each other compared to how much time they spend apart. Finally, these time-stamps can also prove useful for when mutual detection between tags is not available or feasible; in these cases it may be possible to infer potential encounters from the fact that two or more individuals were detected in the same area (and by the same base station) at around the same time.

However, this technology is not without its shortcomings. One of the issues is how to interpret the data received. Since many systems including Encounternet are based on proximity-logging, we are forced to infer encounters between individuals based solely on their distance from one another. While animals that are closer to each other are obviously more likely to interact, Encounternet does not allow us to determine what sort of encounters individuals have engaged in, or even if one has actually taken place. Attaching cameras to the radio tags goes a long way toward resolving this issue, but cameras tend to be prohibitively expensive for many people and can drain the battery life of a tag. Therefore, we propose that a more accessible solution may be to supplement data acquired by Encounternet with live behavioral observations of the same individuals. This way, we can confirm or refute that animals sharing many proximity logs are also more likely to be spotted interacting together in real life, thus providing us with a test of Encounternet's validity.

We recorded how new data on Northwestern Crows can be obtained through innovative combinations of Encounternet and observations. It is our hope that by doing so, we can shed light on the strengths and weaknesses of both methods, and how to better join the two techniques. First, we sought to test the external validity of the Encounternet system itself. Based on past work (Robinette & Ha, 2000), it is known that crows forage on the beach more often during low tides than during high tides. We can confirm the system's validity by analyzing when base stations are detecting tagged birds on the beach compared with the noted tide heights for each day. If the base station logs show appearances by tagged birds on the beach that match up with low tide times, we may be more confident in Encounternet's ability to accurately detect radio tags within range in real time.

Secondly, we used Encounternet's time-stamps to identify resident crows at the beach. Given that Northwestern Crows are territorial, we may assume that those detected on the beach after a certain hour are likely to be roosting nearby. We may also obtain further information on which crows may be roosting together based on which individuals are detected simultaneously in proximate contact with each other. These data may then be compared to live observations to test whether crows detected through Encounternet as potential associates indeed spend more time near each other while foraging. For example, if tagged crows are shown through Encounternet to share many inter-tag encounters and have also been observed interacting frequently while foraging, we can be more confident in interpreting their Encounternet logs as actual social contact. However, if they are not observed as associating particularly with each other, we may conclude instead that the bulk of their shared logs consists of simply proximity data but few real encounters. These inferences would be strengthened by comparing Encounternet and live data collected at simultaneous time periods on the same population of crows on the beach. Combining these approaches may provide more insight into the social organization and foraging strategies of the Northwestern Crow.

Hypotheses: Altogether, we make the following predictions: 1) juvenile Northwestern Crows are less efficient foragers than adults are, 2) juveniles will engage with larger numbers of foraging partners than adults, 3) most foraging associations consist of mixed age classes (juveniles associating with adults, and vice versa), 4) crows are not associating randomly on the beach, and 5) dyads (pairs of individuals) that often interact cooperatively are less likely to behave aggressively toward each other, and vice versa. We also test the Encounternet system's external validity by quantifying the amount of logs detected as a function of tide height, examine the logs for information about roosting and residency data among the tagged crows, and compare the logs to visual observations collected during the same time period on the beach.

Methods:

Subjects: Between January 24, 2006 and July 24, 2013, 44 Northwestern crows were caught with a net launcher (Washington Department of Fish & Wildlife, Permit No. WM-0158; United States Department of the Interior, Fish & Wildlife Service, Permit No. 22802), and each fitted with a unique combination of 2 or 3 colored leg bands and one Fish and Wildlife aluminum band. Individuals are identified by their band combinations, starting from the top band on their left leg and ending with the bottom band on their right leg. Nineteen of these crows also received Encounternet tags (12 in 2012 and 8 in 2013). One bird (tag 23/34, White White – Aluminum Yellow or WW-XY) was caught and tagged twice. Each bird was restrained briefly for banding, aging, and blood draw. We aged the birds according to plumage, mouth color, and overall size (Pyle 1987).

Data for the individual foraging and social associations hypotheses (1 and 2) were collected July 1, 2014 – September 9, 2014, and included both banded and un-banded individuals seen at the beach. Juveniles were defined as crows in their first and second years. A total of 96 (54 adults, 42 juveniles) crows were observed for individual foraging, and 107 (54 adults, 53 juveniles) for social associations.

Research site: Subjects were captured, released, and observed at Meadowdale Beach Park (N 47°, W 122), Snohomish County, Washington.

Hypothesis 1 (individual foraging): Crows were sampled using five-minute focal periods, and we recorded the age, total time spent producing (defined as head down, searching the substrate), total food items consumed, and each food item when identifiable, for each focal bird. To offset possible bias created when a focal crow flew away before the five-minute observation window was over, we measured producing efficiency in the rate of items found per second by dividing each crow’s total items by its total producing time. Because all individuals in our sample found and consumed similarly-sized small food items, handling time differences per item was found to be negligible.

Hypotheses 2 and 3 (social associations): Individuals were sampled in five-minute focal periods as in the Hypothesis 1 methodology. Crows were counted as associating with each other when they remained within five body lengths of each other for over 15 seconds. For each focal crow we recorded their age, total number of partners, and average number of partners per interaction.

Hypotheses 4 and 5 (social networks): All-occurrence sampling was performed on the beach during low tides (Robinette & Ha 2000) from June 4, 2013 to Oct. 3, 2013, using Bushnell spotting scopes mounted on tripods. Behaviors were recorded on datasheets according to an ethogram (Table 1).

Encounternet: Our Encounternet system consisted of three components: 20 microprocessor-equipped radio tags that transmit regular ID pulses, and which receive ID pulses from other tags nearby and log them to memory (Figure 1a); 4 base stations equipped with Yagi antennas placed throughout our research site to monitor and log the presence of tags within radio range (Figure 1b), and collect proximity logs from tags; and a portable "master node" Yagi antenna used to wirelessly collect accumulated proximity logs from base stations, and also to track tagged animals. Twelve of these tags were deployed from Sept. 13, 2012 to Nov. 29, 2012, and the remaining 8 from Apr. 17, 2013 to May 11, 2013. Encounternet tag logs were downloaded from base stations set up around the beach on a weekly basis until the base stations stopped storing tag logs, indicating the tags' batteries were dead.

When 2 or more Encounternet tags came within range of each other, they would record the presence of the other tag(s) as a proximity "encounter" (Rutz et al 2012, supplementary material). According to live field tests, tags could detect each other for up to about 20 m; however, as distance increased the signal strength (measured in "received signal strength indicator", or RSSI, values) decreased, and logs were less likely to be recorded at lower RSSI values. Both tags and base stations that detected other tags were set to record the tag ID and time and date of encounter in their own logs.

Encounternet boasts a very high symmetry or reciprocal rate between tags, meaning that when tags were involved in "encounters" with each other, all tags present recorded the interaction separately in their own logs (bird A → bird B, bird A ← bird B). We evaluated reciprocal entries in our logs for three consecutive days (October 2-4, 2012) when all tags were active and discovered that when only two birds were present there was 100% symmetry in reciprocal tag detections for a total of 121 encounters and 242 logs. When 3 or more tagged birds were present, reciprocal detections were >80% suggesting some system limitations to instantaneous recording when there are multiple simultaneous tag signals, but the accuracy of the two bird situation suggests this is due to "a busy signal" rather than asymmetrical detections in the system. We also looked for symmetry in the received signal strength indicator (RSSI) values between tags across those three sample days. Higher RSSI values are associated with closer tag-tag proximity. Our RSSI values were similar between interacting tags, with some error due to the position of the antenna on each subject and habitat obstructions (Figure 2). We will drop values with RSSI errors greater than 15, as that is the upper cap of most tags' ranges.

Base stations' log dump thresholds were set at 5 logs, meaning that when a tag carrying 5 or more logs came within range of a base station, the base station would automatically initiate a download of the tag's logs. Downloaded logs were cleared from the tag's memory, thus freeing it to generate more logs. Likewise, downloading logs from base stations with the master node cleared the base stations' memories as well. These logs were downloaded weekly through the "master node" into a Netbook using a custom program called Pymaster (developed by John Burt). Pymaster also allowed us to send signals through the master node to any other Encounternet equipment within range if needed to change a tag or base station's settings, or update its firmware.

Tag pulse rates (how often the tag sent out a signal that could be detected by other Encounternet hardware) were set to every 20 seconds. To conserve battery, tags were set to sleep overnight from 9:00 pm to 6:00 am. Base stations were set to sleep from 10:00 pm to 5:00 am.

Data analysis: A Gaussian GLM was run on the individual producing rates for Hypothesis 1 with age as the main independent variable (IV), and tide height and day of year (number of days since January 1, 2014) as covariates to account for ecological and seasonal effects. One outlier of greater than two SDs from the mean was dropped from the final analysis.

For Hypotheses 2 and 3, we ran a Poisson GLM on the total number of social partners with age as the main IV, and tide height and day of year as covariates (similar to our producing model), and a Gaussian GLM on the average number of partners with age as the main IV, and tide height and day of year as covariates. To test whether adults and juveniles were exhibiting homophily or heterophily, we constructed individual dyads from each interaction, consisting of the focal bird and one of its partners, and classified them as adult-adult, adult-juvenile, or juvenile-juvenile interactions. Chi-squared goodness of fit tests were run on all three types of dyads.

For Hypotheses 4 and 5, we used the R package tnet (http://www.r-project.org/) to produce centrality measures and the free Excel add-on NodeXL for graphical representations of our social networks based on observations of banded crows. Centrality measures are analyzed with R. Degree heterogeneity was used as a measure of differential association levels between nodes in our overall associations network, and calculated in two different methods. The first compares the AIC score of row effects to a null model, which assumes random distribution of numbers in the sociomatrix, simulating crows associating at random. We did not include a column effects model because our network is undirected (its sociomatrix is symmetrical), which renders the row and column effects as equivalent to each other. This symmetry also allowed us to generate simple random graphs (SRGs) simulating it by holding the sum of each observed column constant while varying how the edges within that column are distributed. In other words, we hold each node's overall degree constant while randomizing which other nodes it forms edges with. Thus this helps surmount the issue of observer bias by compensating for the possibility that some crows possess higher degrees simply because they were seen more.

We further divided our overall network into separate agonistic and affiliative networks. Agonistic behaviors included Fight, Aggressive Scrounge, Withdrawal, Chase, and Displace; affiliative included Forage Together, Preening, Feeding, Approach, and Arrive. These networks were binarized, where a 1 in the sociomatrix indicated the presence of an affiliative or agonistic interaction between a dyad at any point, and a 0 indicates no such interaction. We then ran a Fisher's exact test between our affiliative and agonistic networks to calculate the odds ratio of the same dyads appearing in both.

To evaluate Encounternet's validity, tide heights for each log recorded between a base station and tag were calculated using a custom software program, which returns an exact tide height per log given its timestamp, the time of the previous high or low tide, and the time of the subsequent high or low tide. After obtaining the specific tide values (in feet) for each encounter, we divided the tide heights into one foot blocks from 4 to 10 feet. For example, a tide height of 5.6 feet would be placed in the "5-6 feet" block. Due to their rarity, tide heights below 4 feet were collectively grouped together, as were those above 10 feet. Due to its distribution, we used the program R to fit a zero-inflated negative binomial regression to the data, entering in tide height as the main IV, and the average tide height change (rising vs. falling, in feet), time of day factors (morning vs. evening and day vs. night), and day of year (for seasonal effects on tide height) as covariates.

"Residency" as detected through Encounternet is defined as crows with tags that were picked up by the base stations at the beach between 19:00 and 6:00 the next day, when we may assume crows are at their overnight roosts. Likewise, two individuals were counted as roosting together if they appear in each other's logs between 19:00 and 6:00.

We counted live observations and base station-tag logs as being collected during "simultaneous time periods" if they were time-stamped within 10 minutes of each other. We then calculated a "percentage of overlap" by taking the number of overlaps over the total number of tagged birds observed on the beach, since live observations were the only method certain to indicate the presence of an individual at the site.

Results:

Hypothesis 1: Neither age ($t(95) = -.82$, $p = .42$) nor the day of year ($t(95) = -.1.86$, $p = .07$) had a significant effect on the rate of production, but crows were significantly more likely to forage at lower tide heights ($t(95) = .2.21$, $p = .03$, Table 2).

Hypotheses 2 and 3: Adults were not solitary significantly more often than juveniles were, χ^2 (1, $N = 26$) = .62, $p = .43$, nor were crows of either age more likely to associate preferentially within their own age class (adults with other adults and juveniles with other juveniles), χ^2 (1, $N = 118$) = 2.17, $p = 0.14$. However, adults and juveniles were significantly more likely to associate with each other than within their respective age classes, χ^2 (2, $N = 291$) = 90.64, $p = < .001$, Figure 3. Juveniles also had more total partners on average than adults did, $z = 3.10$, $p = .002$, Figure 4, but not more average partners per interaction, $t = 1.04$, $p = .30$. There was no significant effect of tide height and day of year on either total number of partners ($z = 1.61$, $p = .11$ and $z = .87$, $p = .39$, respectively, Table 3) or average number of partners ($t = -.09$, $p = .93$ and $t = .88$, $p = .38$, respectively).

Hypotheses 4 and 5: After fitting our social association data to null and row effect models, we received AIC scores of 5665.01 and 4814.87, respectively. Since a lower score indicates a better fit, this model suggests that each row, or individual node's overall degree, in the network has some effect on how the numbers are distributed within the network. Our observed network's degree distribution is also significantly higher that of 1000 SRGs, $p < .001$, Figure 5, meaning there is more heterogeneity in degree that expected under random distribution.

The odds ratio between the affiliative and agonistic networks was 10.74, meaning dyads that appeared in one network were more than 10 times more likely to also appear in the other, $p < .001$, Fisher's Exact Test (FET). When we drop all edges based on two crows simply foraging near one another, our odds ratio decreased to 7.73, $p < .01$, FET. The dyads present on both networks were engaged in only two agonistic interactions, Displace and Move Away, so we ran two post-hoc contingency tests on whether those dyads engaged in either behavior at higher proportions than the background population. Dyads that were both agonistic and affiliative toward each other did not significantly displace ($p > .05$, FET) or move away ($p > .05$, FET) from each other. The odds ratios for the two contingency tables were 1.06 and 1.30, respectively.

Tide heights from Encounternet: Overall, our base stations detected more tags on the beach during higher tides, but according to our zero-inflated negative binomial model, mean tide height had a positive effect on the zero-inflation model, $z = 2.36$, $p = .02$, while morning vs. evening ($z = -9.61$, $p < .001$) and day vs. night ($z = -3.89$, $p < .001$, Table 4a) had a negative effect. Morning vs. evening ($z = 2.52$, $p = .01$) and day of year ($z = 2.68$, $p = .007$, Table 4b) had positive effects on the count model.

Residency and roosting: Eight tags were logged by base stations between the hours of 19:00 and 6:00, and the total number of detections recorded (Table 5). Likewise, each pair of tags recorded together between 19:00 and 6:00 is given in Table 6.

Simultaneous Encounternet and live observations: We had both Encounternet logs and live observations for a total of 13 days. Of the total number of logs, 76.92% showed an overlap of each type of data within 10 minutes of each other. 92.31 % of our observations of crows with active tags had corresponding base station-tag logs. However, all these data consist solely of tag 34 or WW-XY, which was one of only two tags that were still functional at this point.

When we include interaction data taken on all tagged birds at any time in addition to those occurring simultaneously with live observations, we find that only tags 23/34 and 42, or crows WW-XY and BO-RX, share interactions in both the Encounternet (147 logs) and observation (5 interactions) data.

Discussion:

Contrary to our prediction, adult Northwestern crows are not more efficient producers than juveniles in terms of food items found per second. Therefore, juveniles may be close to optimal producers by the time they begin foraging on the beach. Instead, tide height appears to be the main factor affecting foraging efficiency, likely because more food patches are available during lower tides.

Our social association data suggest that there is no affinity among Northwestern crows for partners of their own age; most dyads in fact occurred across age classes. Juveniles also associated with more partners overall compared to adults, but not more partners per interaction, suggesting that they could be engaging in separate interactions more often than adults. This may be due to juveniles' dependence on their adult parents or other relatives prior to reaching maturity, possibly splitting their time between associating with mature kin otherwise foraging separately from each other. Adults in turn might be more willing to tolerate and forage near juvenile relatives than unrelated individuals or other adults. This supports the finding that

Northwestern crows direct aggressive scrounge attempts more often toward less related individuals (Ha, Bentzen, Marsh, & Ha, 2003), and are thus capable of both kin recognition and kin altruism. These results would be bolstered by bloodwork from known individuals observed associating often, to definitively establish kinship.

The significantly higher degree distribution of our observed network compared to chance levels agrees with our social association results and confirms earlier findings (Ha et al., 2003) that crows on the beach are not associating at random while foraging. It also suggests that some individuals may be more social than others, as reflected by their higher degrees within the network (Figure 6). A future step would be to refine our network into a directed one to track the direction of targeted behaviors such as scrounging attempts or dominance displays. Combined with information about banded individuals' sex and age for instance, this could provide us with data on whether certain crows are more likely to perform or receive these behaviors. We may also look at dyad-level covariates, such as whether same-sex pairs are more or less likely to exhibit aggression toward each other, or whether reciprocity and/or the level of relatedness between two individuals affects how likely they are to share food with each other.

Our affiliative and agonistic networks do not seem to be mostly mutually exclusive as predicted, nor do they engage in specific agonisitic interactions at higher proportions than the background population; instead, the dyads present in one network appear to predict the presence of the same dyad in the other network. This may be because crows that are around each other more often and for longer periods of time are simply more likely to engage in interactions together, both aggressive and cooperative. When we removed the observations based solely on individuals foraging in proximity with each other but not engaged in any specific shared behavior, the odds ratio of the two sociomatrices decreased, suggesting that this could be the case. Another factor could be dominance; it is possible that in dyads with both types of interactions present, a dominant crow is acting aggressively toward a subordinate, while the subordinate is directing affiliative behaviors at the dominant as a sign of appeasement. Again, adding nodal and dyadic covariates to the analysis would help clarify whether specific individuals or relationships are more likely to be aggressive or cooperative, and allow us to track the direction of agonism and affiliation to test the dominance theory. Though these results only represent fairly simple SNA methods, they demonstrate the immense potential social networks possess in the field of animal behavior, and as the area of SNA develops further we may uncover more and more uses for it in our own work.

Although at first glance, our base station-tag logs from the 2012 data indicate that more crows are present for longer periods of time at higher tide heights, this could be due first of all to the fact that very low tides (below 4 feet) are less common in the months of October and November. Secondly, when low tide heights do occur, crows could be more likely to forage right along the tideline, which would be further away from the base stations set up on the opposite end of the beach. This would cause the tags to be harder to detect, if not render them out of range altogether. The increased logs we see during higher tides could actually arise from crows foraging nearer the base stations, or roosting in the trees above and/or meadow behind them, resulting in increased detection. Without GPS locators in the tags or complementary live observations in the same time period, there is no definite way for us to conclude that these logs occurred while tagged individuals were on the beach.

On the other hand, our zero inflated negative binary model shows that base stations were more likely to detect tags on the beach at all during lower tides, as well as during the day and in the morning, though whether the tide was rising or falling had no effect. Of the tags detected under these conditions, more were present later on in our observation season and during the morning, which corresponds to the overall decrease in average tide height in the latter half of our field season (August through October), and the crows' habit of visiting the beach earlier in the day (Robinette & Ha, 2000). Furthermore, it is possible that the tide height was significant for our zero-inflation model but not our count model because, as crows are more likely to arrive in larger numbers at lower tides in general, the base stations are more likely to pick up tag signals at low tide but this count is lowered due to tagged birds foraging further away from the stations. It is therefore arguable that Encounternet does indeed give us a more accurate account of the presence of crows on the beach than it initially appears, but again, without GPS locators we must be cautious in interpreting too much from these data.

We may draw some tentative conclusions from our residence and roosting data. The tags detected the most by base stations between 19:00 and 6:00 the next morning, such as 46, 24, and 23, could be inferred to be present at the beach overnight, suggesting that these individual crows are roosting in the area. Furthermore, given that tag 46 is the only one detected by base stations 315 and 316 and the only one not detected by 312, we might assume that this crow did not associate much with the other tagged individuals at night. And indeed, this assumption is supported by the fact that tag 46 does not appear in any other tags' overnight logs. Similarly, the data acquired from our roosting logs could potentially allow us to hypothesize close relationships between the pairs involved. Coupled with DNA information from blood work, we may test if crows sharing many overnight tag logs are related, as in the case of parents and offspring or siblings, or if they are unrelated adults of opposite sexes, which may indicate mates instead. These results can be further bolstered by additional live observations.

A shortfall of the Encounternet pilot data is the discovery that tag pairs which share numerous logs were not always observed interacting live on the beach a greater amount than others. Thus we cannot rule out the possibility that a portion of our logs is simply recording proximity data rather than real interactions between tagged crows. Another disadvantage is that, even if we could be relatively certain that we were capturing mostly actual interactions of individuals, we cannot interpret from Encounternet data what specific types of interactions or behaviors occurred. For instance, affiliative and agonistic behaviors would both be recorded in the same fashion; live observations are invaluable for obtaining information on the quality of interactions rather than just their quantity.

However, it is also possible that the Encounternet inter-tag logs not represented in our live observations occurred off the beach, at times when manual data collection was not possible, giving Encounternet a decided advantage over live observations. Because our system had no way of tracking exact GPS coordinates, we cannot infer from our logs where such encounters took place, outside of rough estimates provided by our base station logs. Therefore, it is possible that, rather than overestimating crow encounters based on proximity instead of interactions, these Encounternet-exclusive logs reveal encounters occurring out of our sight. This is supported by our finding that some of our inter-tag logs consistently boast higher RSSI values despite the pairs not being recorded by observers, indicating that they were fairly close to each other for extended periods of time. We believe that, with adequate numbers of radio tags and/or base stations, a reliable rate of detection between tags and base stations, and possibly some added features such as GPS locators, Encounternet could be a highly valuable tool in data collection, when paired with simultaneous live observations on the same population.

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Table 1

Ethogram of recorded behaviors during live observations

Producing: searching the substrate for prey items (head down), probing and capturing a prey item
Scrounge attempt: taking a prey item from a producer. Each scrounge attempt is also recorded as either *successful* (food item obtained) or *failed* (food item not obtained). • *Passive scrounge attempt*: (quiet ground approach without pursuit/attack) • *Aggressive scrounge attempt*: (noisy approach with pursuit/attack)
Preening: straightening and cleaning feathers of another bird with beak
Feeding: shoving food down the throat of another bird
Begging: making characteristic begging/squawking sound and doing wing quiver)
Forage together: 2+ birds walking along intertidal zone with heads oriented towards substrate. Must be <5 body lengths of each other
Approach: one bird directs its visual and body orientation towards another bird, and approaches it via land or air and gets <5 body lengths from target bird
Withdrawal: one bird directs its visual and body orientation away from a previous social interactor bird, and moves away from it via land or air and gets >5 body lengths from target bird).
Arrive: 2+ birds flying in together and landing <5 body lengths apart
Fight: physically attacking another bird with talons or beak
Displace: One bird dislocates another and takes its spot
Chase: Chasing another bird either on foot or in the air

Table 2

GLM results for producing rate

	Estimate	Std. Error	*t* value	*p* value
Intercept	.10	.03	3.037	.002 *
Age	-.005	.007	-.817	.42
Average Tide Height	.004	.002	2.207	.03 *
Day of Year	-.0003	.0002	-1.857	.07

Table 3

GLM results for social associations

	Estimate	Std. Error	*z* value	*p* value
Intercept	.06	.74	.082	.93
Age	.37	.12	3.108	.002 *
Average Tide Height	.04	.02	1.609	.11
Day of Year	.003	.003	.866	.39

Table 4

a. Zero-inflation model coefficients for Encounternet tag detection

	Estimate	Std. Error	*z* value	*p* value
Intercept	6.56	2.97	2.207	0.03
Mean tide height	0.11	0.05	2.361	0.02*
Height change	-0.31	0.18	-1.777	0.08
Morning vs. evening	-1.61	0.17	-9.607	< .001*
Day vs. night	-1.20	0.31	-3.888	< .001*
Day of year	-0.02	0.01	-2.480	0.01*

b. Count model coefficients for Encounternet tag detection

	Estimate	Std. Error	*z* value	*p* value
Intercept	-2.00	2.13	-0.938	0.35
Mean tide height	0.01	0.04	0.271	0.79
Height change	-0.07	0.12	-0.556	0.58
Morning vs. evening	0.28	0.11	2.515	0.01*
Day vs. night	0.31	0.25	1.238	0.22
Day of year	0.02	0.01	2.675	0.007*
Log(theta)	-0.46	0.10	-4.485	< .001*

Table 5

Individual tags and number of logs detected by each base station

Base station	**Tag**	**Number of logs**
315	46	283
314	46	46
312	43	86
312	42	1
312	29	75
312	27	9
312	26	6
312	24	168
312	23	147

Table 6

Number of logs between each tag pair

Tag 1	**Tag 2**	**Number of logs**
42	48	2
42	29	185
29	27	38
27	24	42
29	26	2
24	26	42
29	24	168
29	28	3
29	23	3
23	28	16

Figure 2

a. A crow with an Encounternet tag

b. A pair of base stations set up at field site

Figure 2

The difference in RSSI values between interacting tags (error) as a function of the average (mean) RSSI between tags.

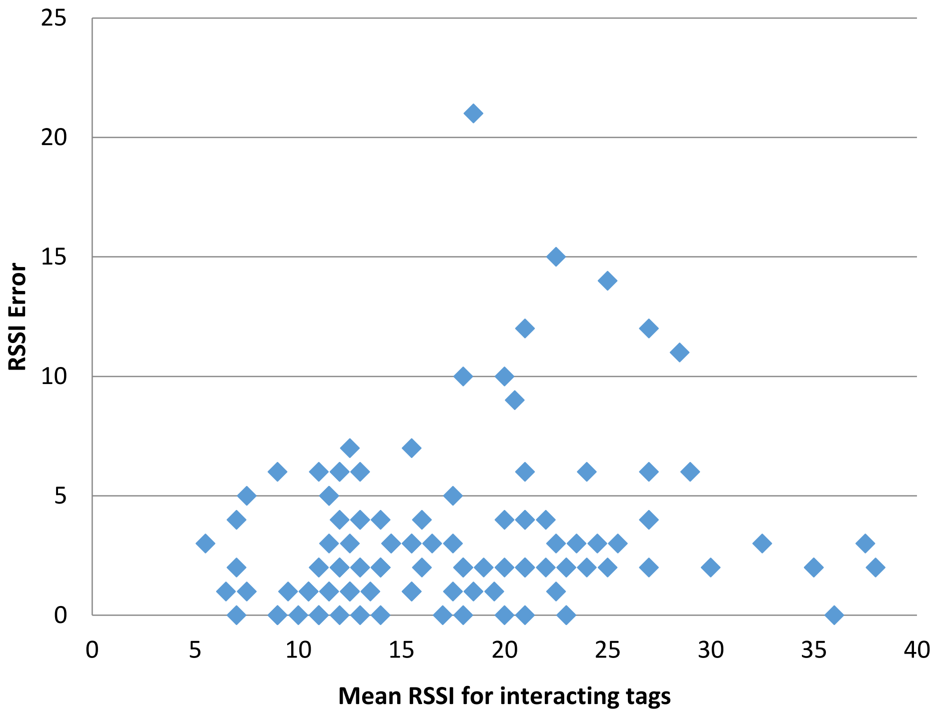


Figure 3

Total number of each type of social association dyad (AA = adult-adult, AJ = adult-juvenile, JJ = juvenile-juvenile)

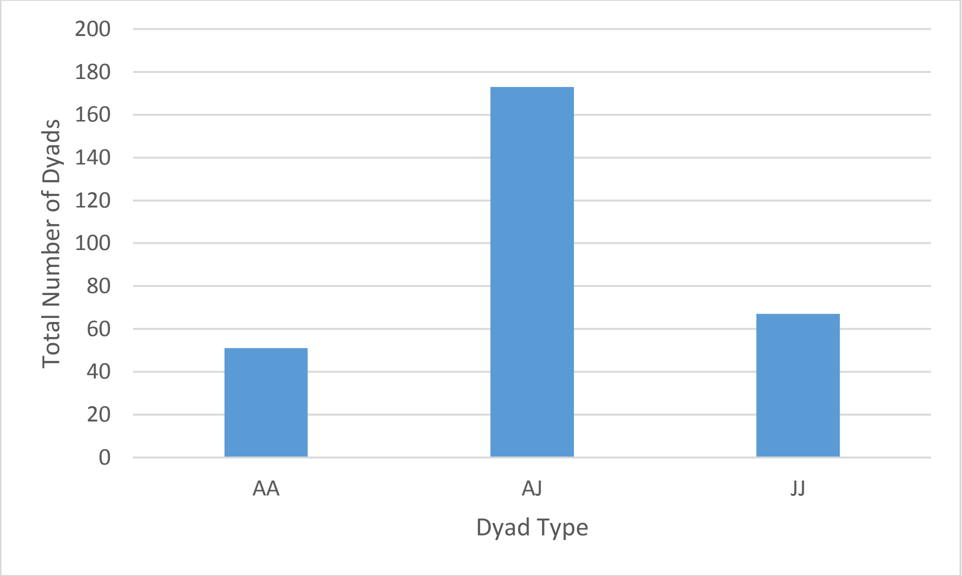


Figure 4

Average number of partners (total) for adults and juveniles. Error bars represent standard error

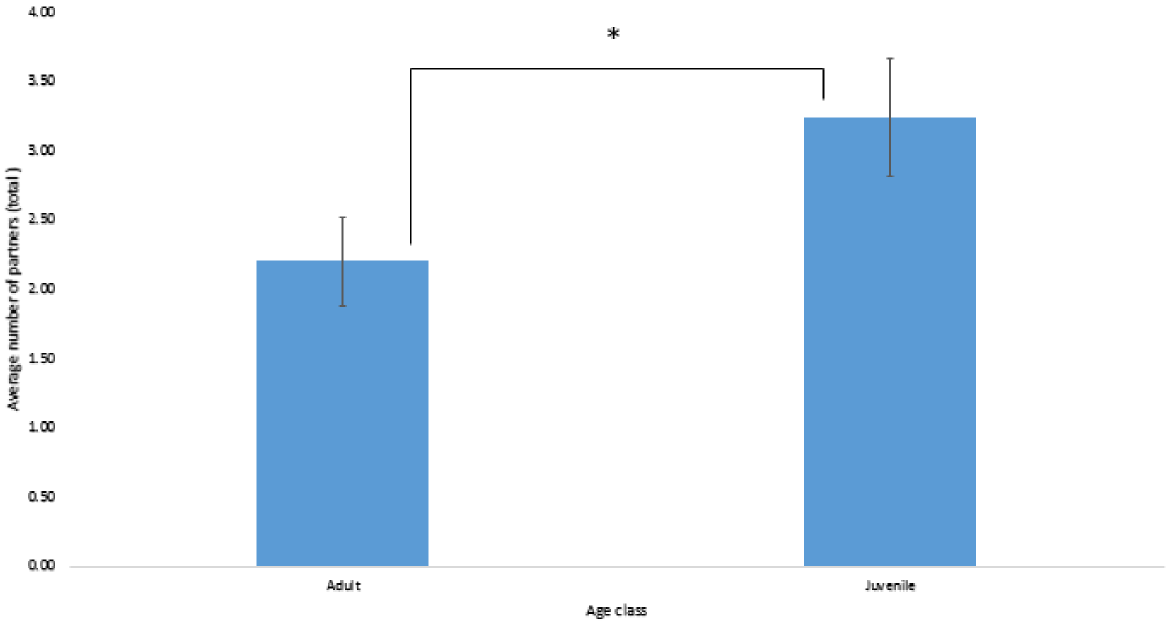


Figure 5

Comparison of observed network's degree distribution (in red) to that of 1000 SRGs (in blue)

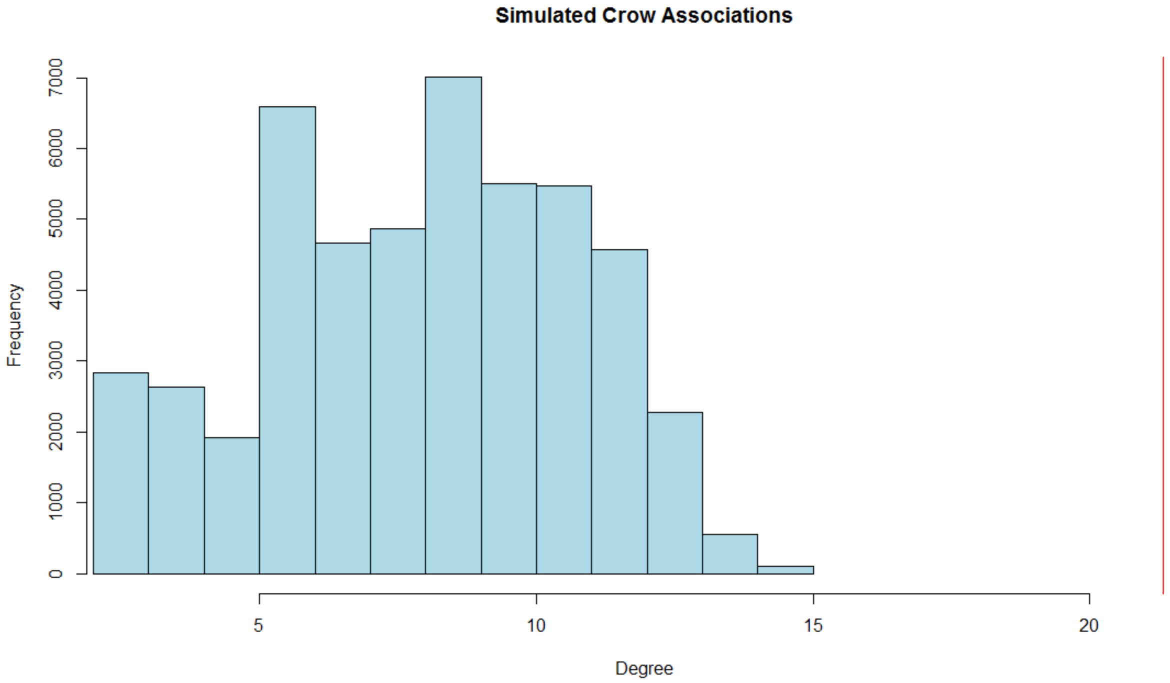
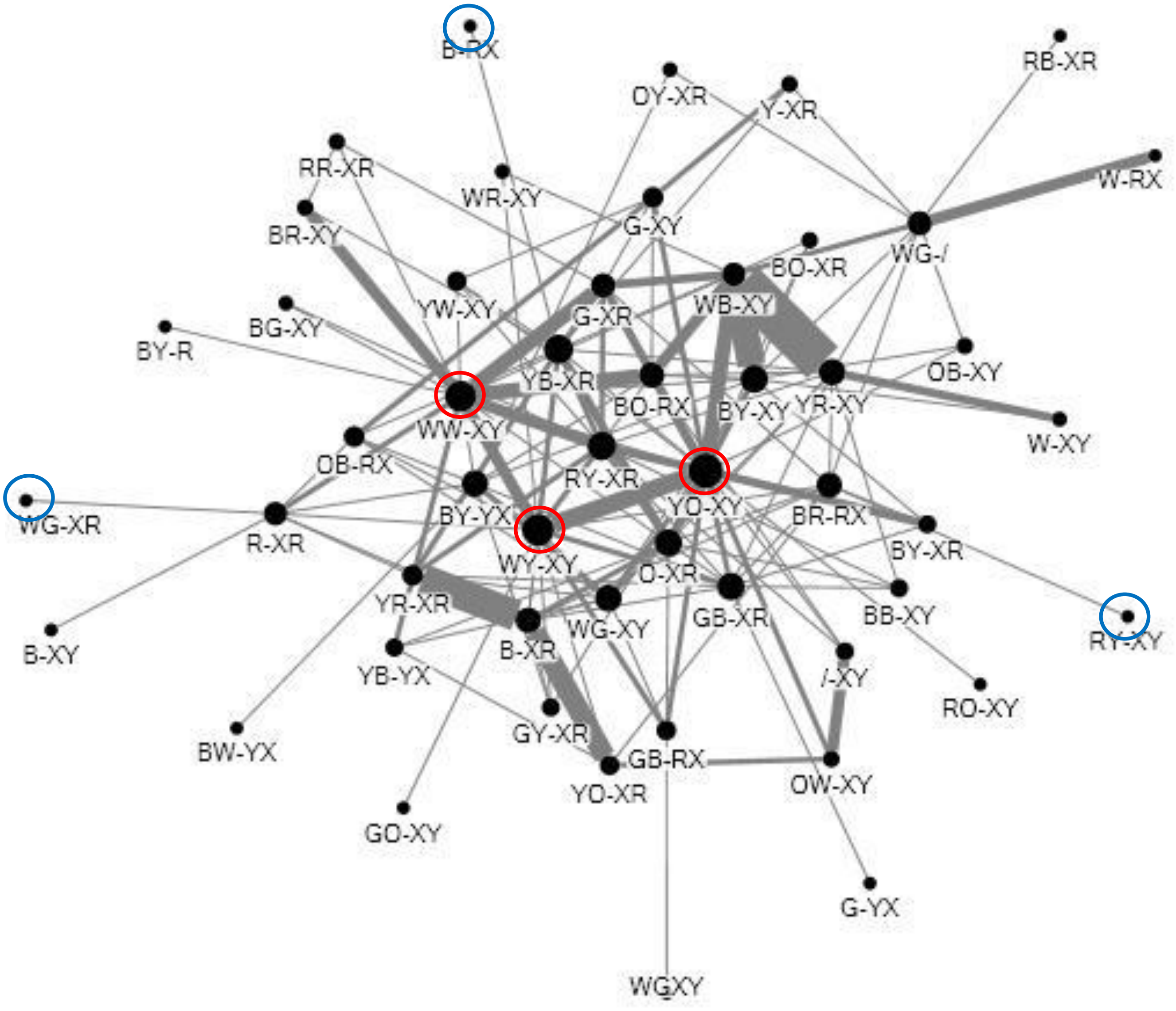


Figure 6

Social network graph of all live observations. Red circles represent nodes with high degree, blue circles represent those with low degree.



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