SUPPLEMENTAL INFORMATION

Automated mapping of social networks in wild birds

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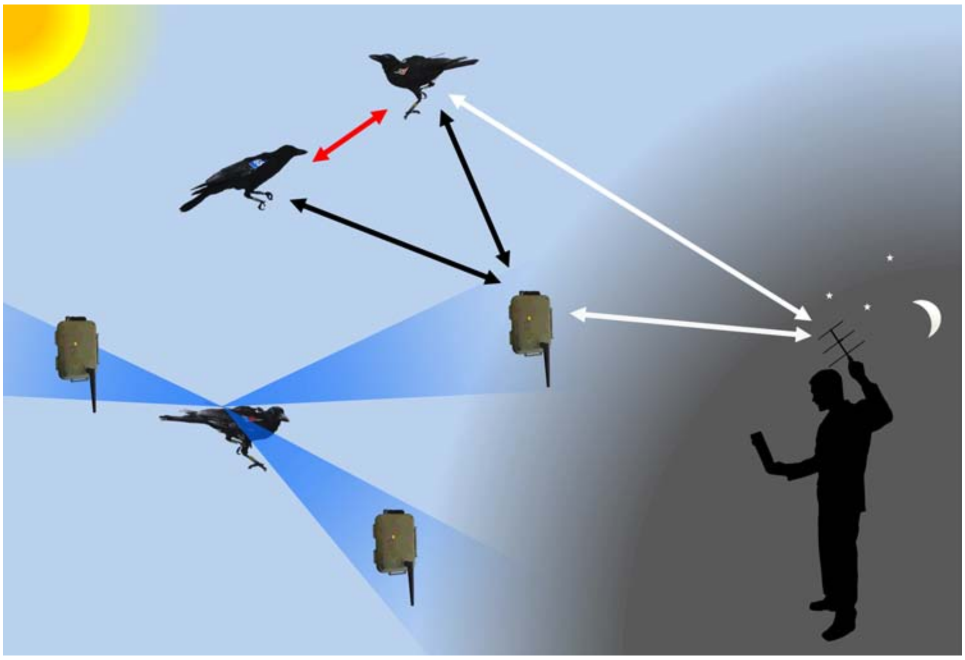

Figure S1, related to Figure 1. Schematic illustration of the rationale and basic operation of the 'Encounternet' system.

Bird-mounted transceiver tags transmit individual identification (ID) codes at a programmed pulse rate, whilst continually 'listening' for signals from other tags. When two or more tagged birds come within detection range (usually several tens of meters), their tags record proximity data for the 'encounter' (as 'received signal strength indicator' values, RSSI) in reciprocal date-, time- and ID-coded logs (red arrow). Meanwhile, whenever tagged birds come within the detection range of 'basestations' (usually *ca.* 100 m), basestations request stored log files from tags and initiate data download, clearing tag memory after successful transfers (black arrows). In addition, basestations log the presence (and RSSI) of transmitting animal-borne tags, so 2D (or even 3D) tag coordinates can later be established through cross-triangulation (indicated by blue triangular shading). Fieldworkers use 'masternodes' to download data wirelessly from basestations or tags, and to communicate with field-deployed hardware as necessary (white arrows), working at night to avoid disturbance to the study system. For example, masternodes can be used to reprogram devices (e.g., resetting of tag pulse rate or duty-cycle parameters), to calibrate hardware clocks for system synchronisation, and to track birds manually in the field through cross-triangulation and homing-in. Note that the schematic is not drawn to scale and that not all possible communication routes between tags, basesations and masternode are shown.

Figure S2, related to Figure 1. Wireless digital transceiver system for the automated mapping of social networks in wild birds ('Encounternet').

(A) Main hardware components of the Encounternet system: miniature transceiver tag, fully packaged for deployment, as used in this study on New Caledonian crows (*bottom left*); autonomous receiver station ('basestation;' opened to show board and D-cell batteries, *bottom middle*, and closed ready for field deployment, *bottom right*); and portable controller unit with 3-element Yagi antenna ('masternode;' *top right*), plugged into a standard 10-inch netbook (*top left*). (B) A basestation deployed in the field. Suspending basestations in the crowns of tall trees, as far away from foliage and large branches as possible, significantly increases tag-to-basestation detection range. (C and D) A wing-tagged wild New Caledonian crow with a harness-mounted transceiver tag. The harness has a 'weak-link' on the breast strap (not visible in the photos) that gradually degrades and safely releases harness and tag after several months. The photos show the same bird (ring code VV2), on 19 October 2011.

Supplemental Experimental Procedures

Wireless transceiver system

Our system ('Encounternet') consists of three self-developed hardware components (Figure S2A): (*i*) miniaturised, animal-borne transceiver tags; (*ii*) autonomous field-deployed receiver stations ('basestations'); and (*iii*) portable controller units with 3-element Yagi antennae ('masternodes'). All hardware is controlled by custom software. The rationale and basic operation of Encounternet is illustrated schematically in Figure S1.

While animal-borne transceiver tags have previously been deployed on mammals (e.g., 'proximity tags' by Sirtrack Ltd., NZ; [S1]), these devices: were too heavy for smaller-bodied species such as flying birds (without collar, *ca.* 20–30 g; collar-mounted, *ca.* 120–500 g); had limited tag-to-tag detection range (*ca.* 30–100 cm, and at best a few meters); and/or needed to be recovered for data download (e.g., [S2–S5]; other systems: 'ZebraNet,' [S6]). Encounternet overcomes these problems, as well as key constraints of other techniques for recording animal association data, including direct observation, mark-recapture protocols, VHF radio-telemetry, GPS tracking, or RFID/PIT systems.

Our tags are small, lightweight, fully programmable and sufficiently energy-efficient for long-term deployment (weeks to months), yet achieve excellent data sampling rates (up to *ca.* 120 proximity detection records per minute), tag-to-tag detection ranges, and onboard data storage (up to 4,000 logs). Two-way communication between all three hardware components (Figure S1) ensures: that mapping of dynamic associations is not spatially constrained (as is the case with systems in which tags only transmit to fixed receiver stations, but not to other roaming tags; [S7,S8]); that animal movements can be tracked in 2D or even 3D space (through basestation cross-triangulation); that tag data can be downloaded wirelessly, either via basestations or directly using a masternode, for 'real-time' analysis (without the need to recapture animals or to recover tags); and that the system can be reprogrammed during field deployment (e.g., to remotely reconfigure tag settings including pulse rate and duty-cycling, or to synchronise tag and basestation clocks). In summary, we believe our project marks the technological breakthrough in recording animal social network data that has been anticipated by several recent reviews [S9–S12].

Over the last few decades, biologists have developed a wide range of innovative packaging and attachment techniques for biologging devices, offering wide taxonomic scope for the application of our Encounternet technology. Apart from being suitable for avian applications, as described here, tags could be attached to leather collars or plastic ear-markers, for mounting on mammals, or designed to be glued non-permanently to reptile skin. As with any other biologging application, configurations need to be assessed on a case-by-case basis, and despite wide applicability, our tags may be unsuitable for certain species, because of either methodological and/or ethical constraints.

Encounternet has a modular design and can serve as a platform for collecting and transmitting other sensor information. We are currently working on the integration of accelerometers, microphones and GPS receivers, and hope to add video cameras and neuro-amplifiers in the future. Encounternet tags with onboard video cameras (*cf.* [S13,S14]) will ultimately enable researchers to distinguish ‘interactions’ from mere ‘associations’ – a long-standing challenge in the field of animal social network analyses (see main text and [S9,S10]).

Tag settings and calibration

Tag parameter settings can be tailored to maximise overall system performance, given known study objectives and constraints. We chose a pulse rate for our tags (one ID-coded radio pulse every 20 seconds, at 433 MHz) that comfortably exceeded the anticipated time scales of fission-fusion events in our crow study system (minutes to tens of minutes), and therefore enabled robust description of biologically meaningful association patterns. Tags ‘opened’ encounter logs when two birds came within signal detection range (i.e., recorded the timestamp of the first received pulse), and ‘closed’ logs (i.e., recorded the timestamp of the last received pulse) when either signal contact had been lost (for more than 120 seconds) or a programmed limit of 300 seconds had elapsed (firmware bugs caused *ca.* 58% of logs to exceed this limit; however, *ca.* 95% of logs lasted less than 340 seconds, while the maximum recorded log duration was 452 seconds). Successive logs were created during extended encounters (see previous note), ensuring that there was no upper limit to recordable encounter length. Proximity information was recorded as ‘received signal strength indicator’ values (RSSI), which in our system are a measure (in integers ranging from *ca.* –20 to +50) of the power ratio (in dB) of the received signal, referenced to one milliwatt. Each encounter log contained a value for each of $RSSI_{min}$, $RSSI_{mean}$ and $RSSI_{max}$. Analyses reported in the main text and Figure 1 are based on $RSSI_{max}$ values (see below).

As will be described in detail elsewhere, we conducted extensive *in-situ* investigations to characterise the performance of our Encounternet system before deployment. An important objective of this work was to generate calibration data, so that tag-recorded RSSI values could later be converted into robust estimates of tag-to-tag/bird-to-bird distances. To this end, we used a fixed array of 12 or 18 tags, each mounted on a dead quail, to run a total of 24 trials, of 15 minutes each, across the five main habitat types in our study area. The resulting calibration dataset enables partitioning of observed RSSI variation into the following variance components: (*i*) tag-to-tag distance; (*ii*) habitat; (*iii*) tag height above ground; (*iv*) relative antenna orientation between tag pairs; and (*v*) residual, unmeasured sources of error.

Networks presented here are based on the presence of dyadic encounters within certain distances as determined from $RSSI_{max}$, with edges weighted according to the number of encounter logs (see below). Multiple encounter logs may result either from repeated independent encounters, or from fewer protracted ones. It is beyond the scope of this paper to distinguish the roles of encounter frequency and duration in determining association strength, but this can be achieved with our dataset by using encounter start- and end-times to calculate encounter durations (integrating across consecutive encounter logs where necessary), and using a refined RSSI-distance calibration fit (weighted according to estimates of crow habitat use and relative antenna orientation) to ascribe a distance, and appropriate confidence interval, to each encounter according to its RSSI values.

Basestation grid

For autonomous data collection, and spatial tracking of tagged birds, we tree-mounted (see Figure S2B) 45 basestations in our study site, with semi-regular spacing along the creeks of two convergent valleys (median nearest-neighbour distance was 93 m, with a range of 59–454 m). Basestations were deployed at above average density (and were programmed to download data only from detected tags that contained ≥ 60 logs) in central areas of high suspected crow activity, and at comparatively lower density (and with a lower download threshold of ≥ 18 logs per detected tag) near the periphery of our study site, to maximise the grid's efficiency at harvesting data from crow-borne tags.

Trapping, tagging and crow attribute data

We used meat-baited whoosh nets [S15] to trap crows non-selectively at four different trap sites in our dry-forest focal study area (Taro and Tabou valleys of Gouaro-Déva; 21°33' S, 165°19' E), on the central west coast of Grande Terre, New Caledonia, South Pacific [S13,S16,S17]. Trapping started on 2 October and ended on 21 October 2011 (pre-breeding and early breeding season) when all traps were removed from the valleys. Diminishing returns from our trap sites, combined with re-sightings of tagged crows, suggest strongly that our sample of 41 tagged birds represented a substantial proportion of the local population, despite the fact that local crow density appears to have increased since earlier work [S17].

Following established protocols, all trapped birds were weighed, measured, and marked with rings and wing-tags [S13,S16,S17]. Encounternet tags were deployed on crows using individually adjusted weak-link harnesses ('one break–all release' design, 1.5-mm braid for large individuals, and 1.2-mm braid for smaller ones; Sirtrack Ltd., NZ; Figure S2, C and D). In an earlier VHF radio-tracking study (unpubl. data), this attachment technique was found to have no observable effects on crow behaviour (subjects habituated very quickly to harnesses and tags) and to release tags reliably and safely after several months; another research group also uses the same harness design for deploying VHF radio-tags on New Caledonian crows [S18]. We chose battery and potting options that ensured that tags had the same dimensions as our earlier, well-tolerated VHF radio-tags, and were so light (9.57 g ± 0.050, 8.90–10.21 g, n = 41; mean ± SE, range) that tag mass was only 3.35% ± 0.062 (2.65–4.07%) of crow body mass, which is well within the range of 3–5% recommended for avian biologging applications [S13,S19,S20]. Harnesses were *ca.* 1 g (small) and *ca.* 2 g (large), respectively, but because body straps were trimmed considerably during the fitting process (individually for each crow), final mass added was significantly lower, and in no case resulted in a combined tag-and-harness mass exceeding the safe limit of 5% of a subject's body mass. For further discussion of ethical considerations, and data indicating excellent survival of tagged crows in our earlier biologging projects, see [S13,S14]. All tagging procedures and field techniques were approved by Oxford University's local ethical review committee (LERC approval granted 22.09.2009) and all relevant local authorities in New Caledonia (permits N°1341-2010/ARR/DENV and N°1886-2011/ARR/DENV; Direction de l'Environnement, Province Sud).

We used 'sex' and 'age' as attribute data for our network nodes (see Figure 1D). Birds were sexed using established molecular techniques (see [S15]; all analyses conducted in R.C. Fleischer's laboratory, Washington DC, USA), and age was inferred from gape colouration, which typically changes from pink to black during the first few years of life (scored as described in [S16]; see also [S21]).

Data collection and processing

The key objective of the present study was to chart potential routes of information transfer in a wild population of New Caledonian crows (see main text). Since this required data from a completely undisturbed group of birds, we applied strict protocols for data collection. Tags were programmed to switch-on at 4:00 hrs on 27 October 2011, to allow all tagged crows—and the population and social network as a whole—five full days to recover from our trapping activities before data collection commenced (during this cooling-off period, heavy construction machinery drove through one study valley briefly in the early morning, and again in the afternoon, but this is unlikely to have affected crows for more than a few minutes; in any case, this traffic ceased before system activation). After the system 'went live,' we visited the study site only at night (i.e., after sunset and before sunrise)—to download logs from basestations, to recalibrate tag clocks and to check tags' log memory (see below)—avoiding any disturbance to the study system. Additionally, present analyses are restricted to the first seven days of data collection, as we subsequently conducted a series of field experiments that caused local perturbation.

After downloading raw log files from basestations, we conducted several checks to ensure data quality. First, we included only birds in our analyses which had, for all seven study days, contributed data from sunrise to sunset, and which had been confirmed to be actively roaming in the study area, i.e., their tags had been recorded by multiple basestations throughout the study area (34 tags fulfilled these criteria; 3 tags had substantially drifting internal clocks, resulting in incomplete data; 4 tags were never recorded, and were either faulty or deployed on birds that had left the study site). Second, for the resulting set of 34 birds, we discarded all data from before sunrise and after sunset (so that networks described activity during daylight hours, and not roosting associations). A frequency distribution of all logged $RSSI_{max}$ values (across the range of values used in this paper) exhibited unexpected ‘troughs’ at 22 and 28, and a ‘peak’ at 25. These anomalies, which are likely attributable to hardware (chipset) properties, do not affect the conclusions of our study.

To assess whether our basestation grid effectively collected data from roaming tags, we conducted two separate analyses. First, examination of basestation data demonstrated that all 34 birds visited many basestations during the study period (across seven days, the median number of different basestations visited per tag ranged between 8 and 11), with only 5 of 238 tag-days (2%) having zero basestation contacts. Second, our nightly checks of crow-borne tags (see above) revealed that tags only ever contained a small number of logs (usually between 100 and 300 logs, with a recorded maximum of 514 logs) and never approached memory capacity, confirming that birds regularly came within reception range of basestations and successfully uploaded their data. Taken together, these *post-hoc* system evaluations indicate that both the basestations’ spacing and sensitivity settings were unnecessarily conservative.

Network analyses

To generate sample networks based exclusively on encounters in which crows approached each other to within known distances, we filtered our quality-checked dataset according to RSSI cut-off values. Inspection of raw calibration data (see above) which were collected under the most ‘favourable’ signal-transmission conditions (tags positioned 4-m above the ground with their antennae oriented in parallel), showed that even under these optimal circumstances, only 2.1% of all pulses received from a distance of 21 m had an RSSI $\geq$ 15 (n = 14 of 670 pulses), and only 5.5% of pulses received from 5.5 m had an RSSI $\geq$ 30 (n = 26 of 471 pulses). Accordingly, we applied an RSSI $\geq$ 15 ‘filter’ (i.e., retaining all logs with $RSSI_{max} \geq 15$) to obtain a dataset for a ‘wide-range’ network, and an RSSI $\geq$ 30 filter for a more restrictive ‘close-range’ network (see Figure 1D). On average, pulse transmissions between bird-mounted tags will occur in less-than-optimal conditions, so the use of our calibration data was extremely conservative and most recorded associations will have been over considerably shorter distances than indicated by our cut-offs. While our technology does not currently permit firm inferences about the biological context of tag-recorded encounters (see above and main text), it is known that New Caledonian crows tolerate other (family and non-family) individuals nearby during tool-use foraging, and rarely express overt/territorial aggression [S17,S18].

After this filtering step, encounter logs (counts pooled across all seven deployment days) were converted into association matrices using R [S22]. Reciprocal entries (bird A → bird B; bird B → bird A) were similar across the whole matrix, with some inevitable deviations (*cf.* [S23]). We symmetrised all final association matrices by using the larger of the two values throughout, as we had no reason to believe that these maximum readings were systematically biased. Edge weights were generated by assigning encounter-log frequencies to one of three bins: high (≥ 10 logs), medium (2–9 logs), or low (1 log); unlike many other field methods, our technology enables the establishment of 'zero' edges with high confidence [S9]. We consider single encounters to be important, given our objective of charting the full range of bird-to-bird social learning opportunities, and our relatively brief study period.

The network parameter of interest in the present study is mean 'node degree,' i.e., the average (or median) number of social partners per crow in our undisturbed, naturally admixing study population (see Figure 1C). For the following reasons, conclusions drawn from this measure are robust to possible methodological issues. First, with respect to our sample of tagged crows, informative analyses require only: (*i*) the inclusion of multiple local crow families; and (*ii*) that birds were trapped non-selectively and were therefore representative of the wider population (both of these conditions were fulfilled; see Figure 1C and above). Thus, the reduction in sample size from 41 to 34 birds, for example, is unproblematic. Second, with respect to our sample of association data, our study is certainly more likely to underestimate, rather than overestimate, node degree, because: (*i*) this measure increases with time (every study day produced a representative description of association patterns, but, as expected, novel dyadic associations continued to be formed as the study progressed); (*ii*) tag recording errors, or any other forms of data corruption, are more likely to result in the loss of true associations than the creation of false ones; and (*iii*) our tags could only record encounters with tagged subjects, so any encounters with untagged crows do not contribute to our summary statistics.

We used UCINET [S24] for basic network analyses, and manually confirmed key results for node degree. Weighted networks were drafted in NetDraw [S25] and subsequently edited in graphics software, showing two node attributes (sex and age; see above). To facilitate visual assessment of node degree and edge weights, as well as comparisons between networks, nodes were arranged in random order on an ellipse, with the same order used for both sample networks (see Figure 1D).

Author Contributions

CR conceived, planned and lead the study, and secured funding; BO, JBu and JBo conceived and developed the Encounternet technology, and are currently working on its commercial exploitation; adaptations for field deployment in New Caledonia were designed by JBu, CR and JSt-C; JBu built basestations and masternodes, and JBu, JSt-C, CR, ZB and SI built tags; CR and JSt-C coordinated fieldwork; CR, JSt-C, ZB, JBu and SI designed protocols for field deployment; CR, JSt-C, ZB and SI conducted fieldwork; ZB managed the database and processed raw data, with support from RJ, JSt-C and CR; CR, JSt-C, ZB and RJ conceived and designed analytical approaches, which were then implemented by ZB and RJ; JSt-C, CR and ZB produced figures, using photos by JSt-C and JBo; CR wrote the manuscript, which was edited by JSt-C, ZB and RJ, and approved by all co-authors.

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