

their mothers. While this might sound unpleasant for the mothers, their milky skin is specially modified for its role in rearing, and mothers are totally unhurt by their rapacious offspring. Although this maternal dermatophagy and extended parental care was only discovered very recently, it may be quite widespread in caecilians and appears to have been around for more than 100 million years.

What is interesting about these amphibians? Caecilians may be most interesting by virtue of their phylogenetic relationships. As their sister group, they are equally as important as Batrachia (all the frogs and salamanders put together) to any attempt to infer features of their common amphibian ancestors and the history of early terrestrial vertebrate life. For example, that all oviparous caecilians lay their eggs on land rather than in water makes it plausible that the last common ancestor of the living amphibians and that of all living tetrapods also practiced terrestrial oviposition. If so, the origin of the amniotic egg would have been preceded by a long history of terrestrial amphibian eggs.

Similarly, recent studies have revealed that frog and salamander skin secretions are rich in bioactive peptides with potential biomedical applications. Given their phylogenetic position, we might expect study of the slimy skin of any caecilian to enhance the known diversity of such compounds more than would study of any additional batrachian. As an independent lineage, caecilians provide many opportunities for comparative biologists to test theories on the evolution of diverse traits that were developed from studies of better-known taxa. For example, caecilian skin feeding and viviparity may provide useful analogues in the study of the evolutionary origins of lactation.

Why are there so few species of caecilians? Good question. Currently there are only about 190 species of caecilian that have been described, compared to more than 600 species of salamander and over 6000 species of frog. Given recent discoveries, the actual numbers of species in each of these groups are far from certain, although the apparent differences in the orders of magnitude in the species diversity of frogs compared

to caecilians and to salamanders is very unlikely to change. Perhaps frog speciation rates have been higher because of their use of song in mate recognition and courtship, or due to occupancy of relatively diverse habitats. In contrast, caecilians have no vocal communication and mostly occupy a more homogenous environment. However, caecilians remain poorly studied taxonomically and many areas in which they occur have been very incompletely surveyed. An entirely new family and radiation of caecilians was found recently in northeast India and it seems entirely plausible that there could be at least twice as many species worldwide as are currently recognised.

I've heard there are global declines in amphibian populations, is that true for caecilians? There have been severe declines, and even extinctions, of some wild populations of frogs and salamanders in recent years. However, despite some anecdotes, there are no good data for caecilians. We do not know if caecilians are troubled by pathogenic chytrid fungus and the IUCN Red List compendium of conservation assessments lists just six caecilian species as threatened while the majority (66%) are 'data deficient'. This ignorance is no basis for being sanguine. Some caecilians seem well-suited to traditional agriculture in the tropics, maintain healthy populations in cultivated areas, and do not seem threatened. In contrast, less adaptable species may have already gone extinct due to changes in land use and large-scale habitat change must be considered a threat to caecilians as it is to many kinds of animal and plant.

Where can I find out more?

- Exbrayat, J.-M. (2006). *Reproductive Biology and Phylogeny of Gymnophiona*. (Enfield, Science Publishers).
- Kamei, R.G., San Mauro, D., Gower, D.J., Van Bocxlaer, I. Sherratt, E., Thomas, A., Babu, S., Bossuyt, F., Wilkinson, M., and Biju, S.D. (2012). Discovery of a new family of amphibians from northeast India with ancient links to Africa. *Proc. R. Soc. Lond. B.* 279, 2396–2401.
- Taylor, E.H. (1968). *The Caecilians of the World*. (Lawrence, Univ. Kansas Press).
- Wilkinson, M., Kupfer, A., Marques-Porto, R., Jeffkins, H., Antoniazzi, M.M., and Jared, C. (2008). One hundred million years of skin feeding? Extended parental care in a Neotropical caecilian. *Biol. Lett.* 4, 358–361.

Department of Zoology, The Natural History Museum, London SW7 5BD, UK.
E-mail: m.wilkinson@nhm.ac.uk

Correspondences

Automated mapping of social networks in wild birds

Christian Rutz^{1,2,*}, Zackory T. Burns^{1,2}, Richard James³, Stefanie M.H. Ismar⁴, John Burt⁵, Brian Otis⁵, Jayson Bowen⁵, and James J.H. St Clair^{1,2}

Growing interest in the structure and dynamics of animal social networks has stimulated major advances [1–3], but recording reliable association data for wild populations has remained challenging. While animal-borne 'proximity' tags have been available for some time [4], earlier devices were comparatively heavy, had limited detection ranges and/or necessitated recovery for data retrieval. We have developed wireless digital transceiver technology ('EncounterNet') that enables automated mapping of social networks in wild birds, yielding datasets of unprecedented size, quality and spatio-temporal resolution. Miniature, animal-borne tags record the proximity and duration of bird encounters, and periodically transfer logs to a grid of fixed receiver stations, from which datasets can be downloaded remotely for real-time analysis. We used our system to chart social associations in New Caledonian crows *Corvus moneduloides* [5,6]. Analysis of ca. 28,000 encounter logs for 34 crows over a 7-day period reveals a substantial degree of close-range association between non-family birds, demonstrating the potential for horizontal and oblique information exchange.

New Caledonian crows use tools to extract prey from deadwood and vegetation, exhibiting remarkable behavioural sophistication [5]. The species is suspected to transmit tool-related information through cultural processes, with crows learning from each other how to make or deploy certain tool types [6]. Our biologging system overcomes difficulties of observing New Caledonian crows in their natural habitats [7] and enabled us to address two main objectives: to chart opportunities for social learning over a range of encounter distances; and to investigate whether social information is

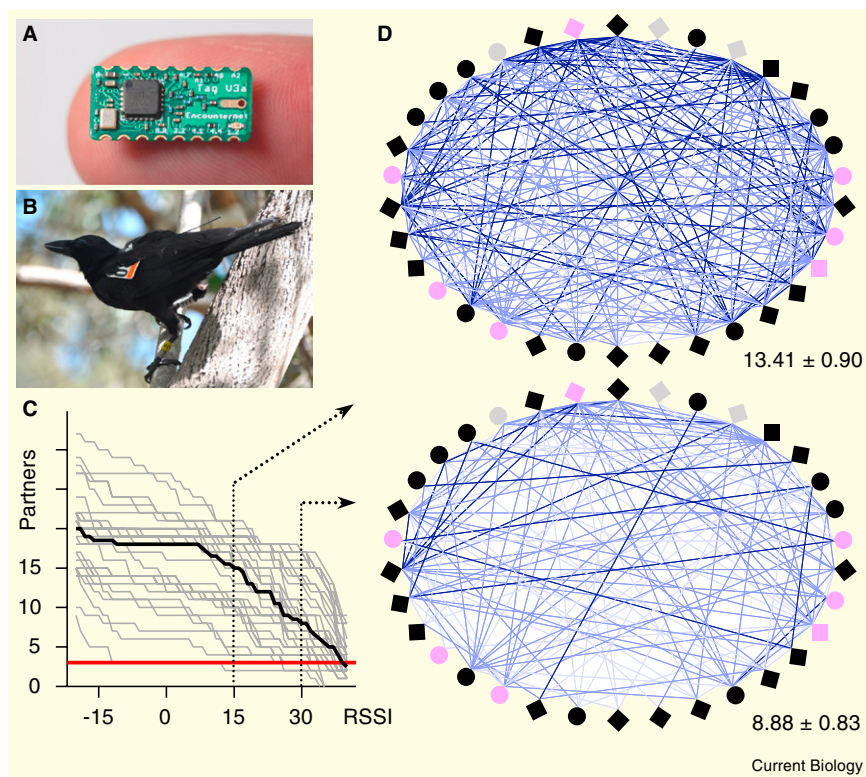


Figure 1. Automated mapping of social networks in wild birds.

(A) Miniature transceiver board with an ultra-low power microprocessor (<0.3 g; on the tip of an index finger for scale). (B) A wild New Caledonian crow with a harness-mounted transceiver tag. (C) Number of social partners ('node degree') as a function of minimum bird-to-bird distance (as measured by tag-recorded 'received signal strength indicator' values, RSSI; grey, $n = 34$ individual crows; black, median for network). The horizontal red line indicates the maximum degree expected if crows only associated with members within core family units (three), and vertical dotted lines mark the RSSI cut-off values used for generating sample networks. (D) Examples of a 'wide-range' network (edges represent at least one encounter of within ca. 21 m over 7 days; top) and a 'close-range' network (within ca. 5.5 m; bottom), with respective degree statistics (mean \pm SE). In both cases, all birds are part of a single interconnected network. Nodes are arranged in random order on an ellipse (same for both networks) and coded according to sex (square, male; circle, female) and age (pink, juvenile; grey, immature; black, adult); edge 'weight' is shown in three increasingly dark shades of blue for (1), (2–9), and (≥ 10) encounter logs.

likely to flow between family groups — a process that may be essential for the effective cultural accumulation of innovations [8].

From 2 to 21 October 2011, we deployed miniature transceiver tags (9.57 ± 0.050 g, mean \pm SE; Figure 1, Supplemental information) on 41 crows at one of our study sites in New Caledonia [7]. Tags were programmed to switch on synchronously after a 5-day cooling-off period, to allow the population to equilibrate after our trapping activities, operating thereafter on a 16-hour wake-time duty cycle (4:00–20:00 hrs). Active tags emitted ID-coded radio pulses every 20 seconds, whilst continually 'listening' for other nearby tags. Whenever two or more tagged crows came within detection range (usually several tens of meters), their

tags recorded proximity data for their 'encounter' (as 'received signal strength indicator' values (RSSI), later allocated to distance classes using calibration data) in reciprocal date-, time- and ID-coded log files (Supplemental information). For sustained encounters, several pulses were combined into a single log file (covering a maximum of 452 seconds), providing minimum, mean and maximum RSSI values for analysis, and allowing an estimate of encounter duration (Supplemental information). Here, we use the shortest physical distance logged between crow dyads, derived from $RSSI_{max}$, to chart opportunities for social learning. Since our technology cannot record the biological context of tag-recorded encounters, we refer here to 'encounters' or 'associations,' rather than 'interactions' [2,3] (integration

of miniature video cameras could overcome this limitation; Supplemental information). A fixed grid of 45 tree-mounted 'basestations' was used to harvest data from roaming tags in the study area and to monitor the locations of tagged subjects (detection range usually ca. 100 m; Supplemental information). For *ad-hoc* network analyses, fieldworkers regularly downloaded data from basestations, working at night to avoid disturbance. While our system generated association data for ca. two months, we focus here on the first seven days, during which the network was entirely undisturbed. In this time period (>90 daylight hours), we accumulated, for 34 crows, some 28,000 unique bird-to-bird association logs and some 190,000 bird-to-basestation logs. It would have been impossible to generate datasets of comparable spatio-temporal resolution and information content with conventional techniques (Supplemental information).

Our technology uncovered a dynamic social system. While crows can gather some social information over larger distances, close-range bird-to-bird interactions may be necessary for the transmission of specific tool-related information [8]. We show that rich association patterns were present both in 'wide-range' networks, with encounter distances of up to ca. 21 m, as well as in 'close-range' networks, containing only encounters of within ca. 5.5 m where direct observation of tool-oriented behaviour would be feasible (Figure 1D). Notably, over a wide range of minimum encounter distances, birds had many more social partners on average (Figure 1C) than would be expected for crow families of 3.22 ± 0.22 individuals ($n = 9$ families) [9], indicating greater potential for horizontal and oblique transmission processes than previously inferred from observations at artificial feeding sites [9]. Although some dyads were only weakly associated, and many encounters will have occurred in non-foraging contexts, the fact that most birds consorted so widely within just a few days illustrates considerable scope for information flow in crow populations. Our study sets the scene for detailed analyses of the roles of individual animals, and network topologies, in driving the diffusion and diversification of cultural information in wild animal societies [10].

Encounternet will be useful in a wide range of contexts to obtain a comprehensive record of dynamic

animal associations. The technology is suitable for long-term deployment on relatively small animals, and overcomes key constraints of other data-collection methods. Importantly, with its high sampling rates and excellent tag-to-tag detection range, Encounternet can generate time-resolved association data needed to link network topologies to biological processes — a key challenge in social network analyses [2,3].

Supplemental Information

Supplemental information including experimental procedures and two figures can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2012.06.037>.

Competing Interests

Encounternet was conceived and developed at the University of Washington, Seattle, USA, and BO, JBU and JBo are currently working on the technology's commercial exploitation.

Acknowledgments

We thank C. Lambert, T. Mennesson and J.-E. Lombardet for facilitating field logistics, C. Anagnostou for field assistance, W. Loo for help with R-code, R.C. Fleischer for molecular sexing, the BBSRC for funding (grant BB/G023913/1 to CR), and the Province Sud and SEM Mwe Ara for generous support in New Caledonia.

References

1. Krause, J., and Ruxton, G.D. (2002). *Living in Groups* (Oxford: Oxford Univ. Press).
2. Whitehead, H. (2008). *Analyzing Animal Societies* (Chicago: Chicago Univ. Press).
3. Croft, D.P., James, R., and Krause, J. (2008). *Exploring Animal Social Networks* (Princeton: Princeton Univ. Press).
4. Rutz, C., and Hays, G.C. (2009). New frontiers in logging science. *Biol. Lett.* 5, 289–292.
5. Hunt, G.R. (1996). Manufacture and use of hook-tools by New Caledonian crows. *Nature* 379, 249–251.
6. Hunt, G.R., and Gray, R.D. (2003). Diversification and cumulative evolution in New Caledonian crow tool manufacture. *Proc. R. Soc. B* 270, 867–874.
7. Rutz, C., Bluff, L.A., Weir, A.A.S., and Kacelnik, A. (2007). Video cameras on wild birds. *Science* 318, 765.
8. Laland, K.N. (2008). Animal cultures. *Curr. Biol.* 18, R366–R370.
9. Holzhaider, J.C., Sibley, M.D., Taylor, A.H., Singh, P.J., Gray, R.D., and Hunt, G.R. (2011). The social structure of New Caledonian crows. *Anim. Behav.* 81, 83–92.
10. Whitehead, H., and Lusseau, D. (2012). Animal social networks as substrate for cultural behavioural diversity. *J. Theor. Biol.* 294, 19–28.

¹Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK.

²Present address: School of Biology, University of St Andrews, St Andrews KY16 9TH, UK.

³Department of Physics, University of Bath, Bath BA2 7AY, UK. ⁴School of Biological Sciences, University of Auckland, PB 92019, Auckland 1142, NZ. ⁵Department of Electrical Engineering, University of Washington, Seattle, WA 98195-3770, USA.

*E-mail: christian.rutz@st-andrews.ac.uk

Wingless virgin queens assume helper roles in *Acromyrmex* leaf-cutting ants

Volker Nehring^{1,2,*},
Jacobus J. Boomsma¹,
and Patrizia d'Ettore^{1,3}

Division of labour is the hallmark of advanced societies, because specialization carries major efficiency benefits in spite of costs owing to reduced individual flexibility [1]. The trade-off between efficiency and flexibility is expressed throughout the social insects, where facultative social species have small colonies and reversible caste roles and advanced eusocial species have permanently fixed queen and worker castes. This usually implies that queens irreversibly specialize on reproductive tasks [2]. Here, we report an exception to this rule by showing that virgin queens (gynes) of the advanced eusocial leaf-cutting ant *Acromyrmex echinator* switch to carrying out worker tasks such as brood care and colony defence when they fail to mate and disperse. These behaviours allow them to obtain indirect fitness benefits (through assisting the reproduction of their mother) after their direct fitness options (their own reproduction) have become moot. We hypothesize that this flexibility could (re-)evolve secondarily because these ants only feed on fungal mycelium and thus could not benefit from cannibalising redundant gynes, and because queens have retained behavioural repertoires for foraging, nursing, and defense, which they naturally express during colony founding.

Permanence of caste is the most fundamental difference between eusocial and cooperative breeding [2]. Helpers of the latter category may become breeders later in life and thus retain full flexibility towards the eventual pursuit of direct fitness. Illustrative examples are cooperatively breeding birds, paper wasps and some Ponerinae ants [3–5]. Workers of eusocial ants and honeybees, by contrast, at best retain some phenotypic

plasticity for adopting specific behaviours depending on their age and the needs of the colony [6], but their reproductive potential is always permanently reduced. The behavioural repertoires of queens tend to be limited to mating, colony founding and egg-laying, and this never changes in response to queen condition. This should imply that gynes — unmated virgin queens — should be cannibalized or otherwise disposed of when they somehow fail to disperse on a mating flight, similar to infertile diploid males [7,8]. Uselessness for both colony-founding and altruistic behaviour means that failed queens have zero fitness and might thus be even expected to die voluntarily, as recycling of their tissues and prevention of further consumption of scarce resources will offer them at least some indirect fitness when their resources will benefit properly endowed siblings.

We observed field colonies of the leaf-cutting ants *Acromyrmex echinator* and *A. octospinosus* that contained several non-inseminated wingless gynes besides the mother queen (Supplemental Information published with this article online). As these queens had been allowed to live, we hypothesized that they might still be worth their keep if they would assume helper roles that were of value for their colony. To test this hypothesis, we experimentally removed the wings of normal gynes and quantified worker-like behaviours. As controls, we used both completely un-manipulated gynes, and gynes with one middle leg removed. This mutilation was not expected to affect normal behaviour as queens missing a leg are occasionally observed as functional colony mothers.

Acromyrmex gynes with their wings experimentally removed were more likely to conduct worker tasks: unlike the control gynes, they took care of brood that we introduced into experimental nests (Figure 1A,B) and they attacked non-nestmates (Figure 1C). A second nestmate recognition experiment, in which tethered gynes were presented with nestmate or non-nestmate odour, showed that both the control and wingless gynes were equally able to discriminate between nestmate and non-nestmate cues (Figure 1D).